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Coordonnées – contact :

Alain Bertrand, Abéla, 09320 Boussenac 07 86 72 06 53 abela11@wanadoo.fr

Using Environmental DNA to Survey Bivalves in Agricultural Freshwater Marshes on the Atlantic Coast

Vincent BOUTIFARD[1], Lilia MZALI[2]

[1] INRAE, UE Saint-Laurent-de-la-Prée, 545 route du bois Mâche, 17450 Saint-Laurent-de-la-Prée, France, e-mail : vincent.boutifard@inrae.fr

[2] INRAE, UE Saint-Laurent-de-la-Prée, 545 route du bois Mâche, 17450 Saint-Laurent-de-la-Prée, France, e-mail : lilia.mzali@inrae.fr

Abstract - Environmental DNA (eDNA) sampling using the metabarcoding method was conducted in five agricultural freshwater marshes located in the Atlantic coast of France to detect freshwater bivalve species. This method had not previously been tested in such environments. A total of seven species were detected: *Anodonta anatina* (Linnaeus, 1758), Anodonta cygnea (Linnaeus, 1758), *Sinanodonta woodiana* (I. Lea, 1834), *Corbicula* sp. (O.F. Müller, 1774), *Dreissena polymorpha* (Pallas, 1771), *Mytilopsis leucophaeata* (Conrad, 1831), and *Sphaerium lacustre* (O.F. Müller, 1774). Among these, *Sinanodonta woodiana* (I. Lea, 1834) was identified as an invasive exotic species, which poses a threat to the local *Anodonta* species. This study demonstrates the potential of metabarcoding-based eDNA monitoring for detecting freshwater bivalves in marsh environments and highlights the presence of invasive species that may impact native populations.

Key words - Environmental DNA (eDNA), Freshwater bivalves, Biodiversity monitoring, Water management, Species detection, Agricultural Freshwater Marshes, French Atlantic Coast

Résumé - Des prélèvements d'ADN environnemental (ADNe) ont été réalisés en utilisant la méthode du metabarcoding dans cinq marais doux agricoles situés sur la façade atlantique en France, dans le but de détecter les espèces de bivalves dulçaquicoles. Cette méthode n'avait jusqu'alors pas été testée dans ce type de milieu. Un total de sept espèces a été détecté : *Anodonta anatina* (Linnaeus, 1758), *Anodonta cygnea* (Linnaeus, 1758), *Sinanodonta woodiana* (I. Lea, 1834), *Corbicula* sp. (O.F. Müller, 1774), *Dreissena polymorpha* (Pallas, 1771), *Mytilopsis leucophaeata* (Conrad, 1831) et *Sphaerium lacustre* (O.F. Müller, 1774*).* Parmi ces espèces, *Sinanodonta woodiana* (I. Lea, 1834), une espèce exotique envahissante. Cette étude montre le potentiel de la méthode du metabarcoding basée sur l'ADNe pour la détection des bivalves dulçaquicoles dans les marais et met en évidence la présence d'espèces invasives susceptibles d'impacter les populations d'espèces locales.

Mots clés - ADN environnemental (ADNe), Bivalves dulçaquicoles, Surveillance de la biodiversité, Gestion de l'eau, Détection des espèces, Marais doux agricoles, Littoral Atlantique

Introduction

Agricultural freshwater marshes along the Atlantic coast of France, covering approximately 200,000 hectares from Morbihan to Gironde, represent critical multifunctional ecosystems. These wetlands require sophisticated water management strategies to balance agricultural practices, tourism, and biodiversity conservation (PREAU *et al.*, 2022). The MAVI project (Maintenir les marais vivants face au changement climatique), led by INRAE Saint-Laurent-de-la-Prée in Charente-Maritime, focuses on assessing the impacts of water management on biodiversity.

Despite their ecological significance, freshwater mollusks remain an underexplored taxonomic group in these marshes, with substantial gaps in knowledge regarding their distribution and ecological roles (BODIS *et al.*, 2011). In Charente-Maritime, JOURDE (1997) provided a comprehensive catalog of freshwater mollusks, which remains a critical reference. Subsequent studies have contributed to our understanding of *Margaritifera auricularia*, particularly in terms of its biology, ecology, and conservation (PRIE *et al.* LEFEBVRE *et al.*, 2014; LAMARRE *et al.*, 2007; BOUVERET *et al.*, 2011; JOURDAIN *et al.*, 2015; DUFRESNE *et al.*, 2019). Freshwater mollusks play essential roles in ecosystem functioning, such as in water filtration and nutrient cycling (STRAYER *et al.*, 2014). Species like the European bitterling (*Rhodeus amarus* (Bloch, 1782)) depend on freshwater bivalves for reproduction, as their larvae develop within the gills of unionid mussels (REICHARD *et al.*, 2007).

Environmental DNA (eDNA) is an emerging tool that allows for non-invasive species detection in aquatic ecosystems (CRISTESCU & HEBERT, 2018). This method has shown success in monitoring fish and invertebrate populations in riverine environments (THOMSEN & WILLERSLEV, 2015). However, its potential for surveying freshwater bivalves in marsh ecosystems remains underutilized. This study aims to intégrale eDNA-based techniques into biodiversity monitoring of agricultural freshwater marshes, enhancing the detection of mollusk species and supporting more effective conservation efforts. The results of our field trials using eDNA to assess bivalve biodiversity in these marshes are presented herein.

Materials and Methods :

Environmental DNA (eDNA) samples are collected from five pilot sites located in the departments of Vendée and Charente-Maritime: Marais de la Vacherie, Marais de Voutron, Marais de Saint-Laurent-de-la-Prée, Marais du Transbordeur, and Marais de Brouage (figure 1). These sites are part of the Atlantic coastal marshes, which extend from the Loire estuary to the Gironde.

All these marshes have been significantly modified by human activities over the centuries. They have been exploited first for salt production gradually abandoned. Currently, the study sites are primarily covered by natural grasslands used for livestock farming, including cattle for meat production, horses, and sheep.

These marshes are traversed by a dense network of channels and structures that control water levels in the channels and the flooding status of the plots. Managers operate them according to the seasonal needs of human activities. In winter, water is drained into the sea, and in summer, the marshes are replenished with freshwater from rivers. (figure 2).

Hydrological flows within the canals are minimal, and the water (fresh or mildly brackish) exhibits high turbidity. The predominance of clay-rich soils promotes sediment accumulation, resulting in significant silting and shallow water bodies rarely exceeding one meter in depth. Furthermore, the waters are heavily nutrient-enriched, creating favorable conditions for eutrophication processes (MASCLAUX *et al.,* 2015).

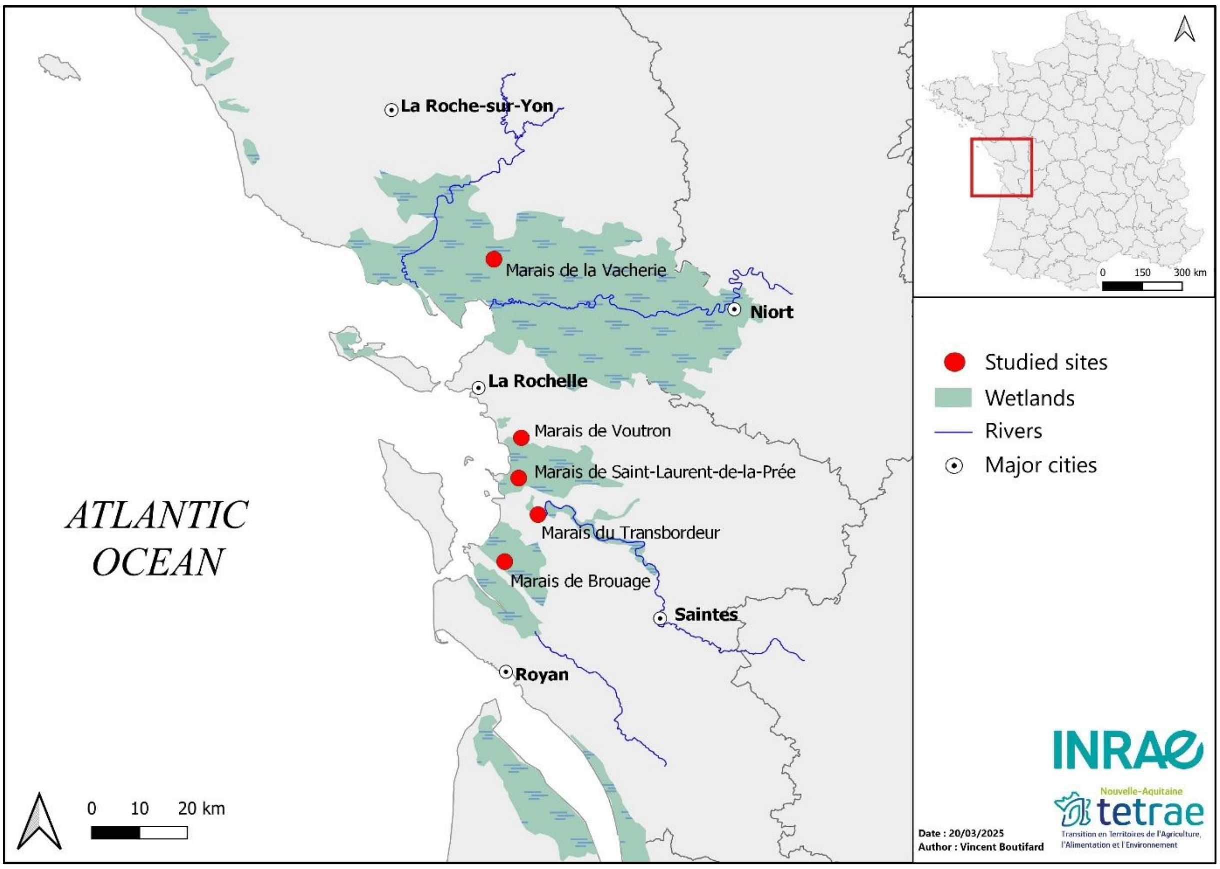
La Roche-sur-Yon
Marais de la Vacherie
Niort
La Rochelle
Marais de Voutron
Marais de Saint-Laurent-de-la-Prée
Marais du Transbordeur
Marais de Brouage
Saintes
Royan
ATLANTIC OCEAN
0 10 20 km
0 150 300 km
Studied sites
Wetlands
Rivers
Major cities
Date : 20/03/2025
Author : Vincent Boutifard

Figure 1 : Map of the study area, including the locations of the sites

The samples are collected between May 24 and 26, 2024, along packraft transects approximately 400 to 600 meters in length, following the SPYGEN® VigiDNA M protocol, which is based on the Metabarcoding approach. The objective of traversing these transects in stagnant water environments is to capture as much environmental DNA as possible present in the water column.

DNA extractions are carried out in a dedicated facility designed for handling rare or degraded DNA. DNA amplification is then performed using two pairs of universal primers specific to bivalves, with 12 replicates per sample and per primer pair. The amplified products are subsequently sequenced using a next-generation sequencer. Throughout each protocol step, negative controls are included alongside the samples to monitor the purity of the consumables and detect any potential cross-contamination during handling.

The resulting sequences are analyzed with bioinformatics tools to correct errors arising from amplification or sequencing (using various filters) and to compare each sequence against the SPYGEN® and GenBank® (version 247) reference databases. A species list is compiled for each sample based on the reference database, detailing the number of DNA sequences and the number of positive replicates attributed to each species. In cases where species exhibit identical DNA sequences within the studied region, differentiation may not be possible. In cases where species exhibit identical DNA sequences within the studied region, differentiation may not be possible. In such instances, species are identified at the genus or family level, particularly for Asian corbiculids, such as *Corbicula fluminea* (Müller, 1774), *Corbicula japonica* (Petit de la Saussaye, 1852), and *Corbicula fluminalis* (O. F. Müller, 1774).

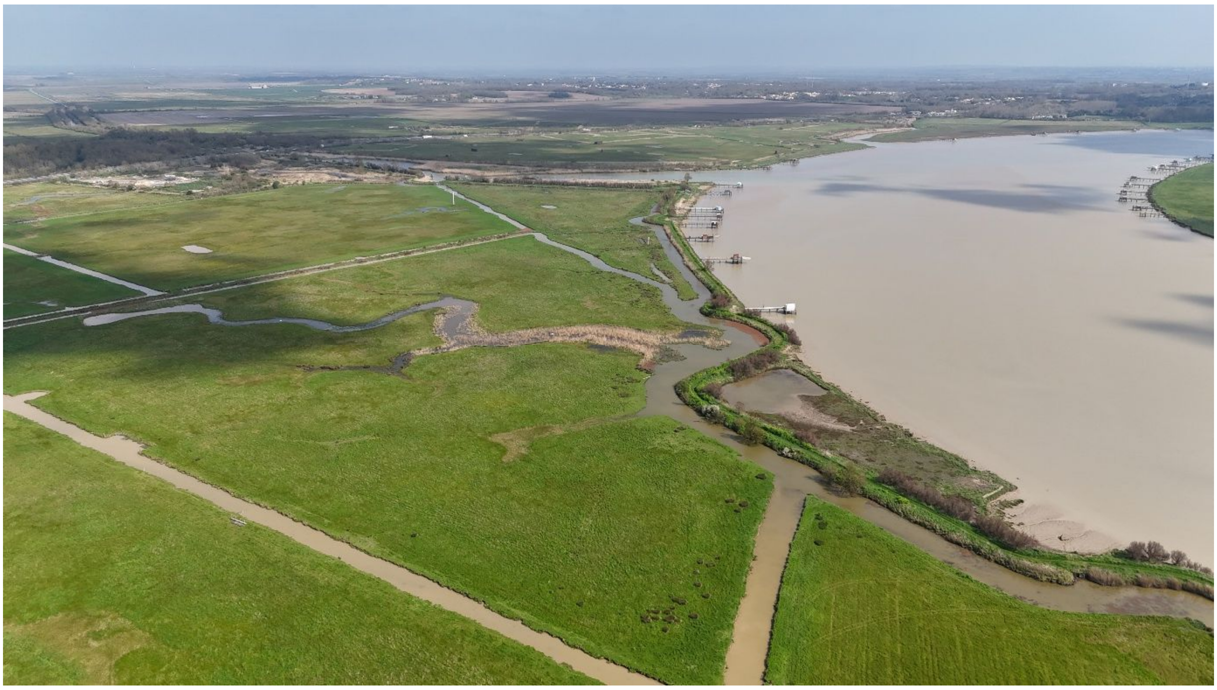

Figure 2 : Aerial photograph of the freshwater marsh of Saint-Laurent de la Prée, France. The pasture plots are bordered by channels that act as fences ©INRAE 2025.

Results :

A total of seven freshwater bivalve species were detected across the five study sites. Three species belong to the family Unionidae, while two species are part of the family Dreissenidae. The families Cyrenidae and Sphaeriidae are each represented by a single species.

Table 1 presents the detection of these bivalve species across the five marshes. The presence of each species is quantified based on the detection of DNA base pairs, categorized as follows: (+) for 100 to 1,000 DNA base pairs, (++) for 1,000 to 10,000 DNA base pairs, and (+++) for more than 10,000 DNA base pairs.

Table 1 : Detection of freshwater bivalve species across five marshes based on DNA analysis.

Species	Marais de la Vacherie	Marais de Voutron	Marais de Saint-Laurent de la Prée	Marais du Transbordeur	Marais de Brouage
Anodonta anatina (Linnaeus, 1758)	**-**	**+++**	**-**	**-**	**++**
Anodonta cygnea (Linnaeus, 1758)	**-**	**++**	**-**	**-**	**-**
Sinanodonta woodiana (I. Lea, 1834)	**+**	**+++**	**++**	**-**	**++**
Corbicula sp. (O.F. Müller, 1774)	**-**	**-**	**+**	**-**	**+**
Dreissena polymorpha (Pallas, 1771)	**-**	**-**	**+++**	**-**	**-**
Mytilopsis leucophaeata (Conrad, 1831)	**-**	**-**	**-**	**-**	**+++**
Sphaerium lacustre (O.F. Müller, 1774)	**-**	**++**	**-**	**-**	**-**
Species richness	**1**	**4**	**3**	**0**	**4**

Among the Unionidae family, *Anodonta anatina* (Linnaeus, 1758) is highly detected in Marais de Voutron (+++) and Marais de Brouage (++), while *Anodonta cygnea* (Linnaeus, 1758) is found exclusively in Marais de Voutron (++). *Sinanodonta woodiana* (I. Lea, 1834) exhibits high detection levels in Marais de Voutron (+++), Marais de Saint-Laurent-de-la-Prée (++), and Marais de Brouage (++). Notably, it is the only species detected at four sites.

Corbicula sp. (O.F. Müller, 1774) (Cyrenidae) is detected at lower levels in Marais de Saint-Laurent-de-la-Prée (+) and Marais de Brouage (+). *Dreissena polymorpha* (Pallas, 1771) (Dreissenidae) is highly present (+++) in Marais de Saint-Laurent-de-la-Prée, whereas *Mytilopsis leucophaeata* (Conrad, 1831) is detected at high levels (+++) exclusively in Marais de Brouage. Lastly, *Sphaerium lacustre* (O.F. Müller, 1774) (Sphaeriidae) is found in Marais de Voutron (++) but is absent from the other sites.

Species richness varies among the marshes, with Marais de Voutron and Marais de Brouage exhibiting the highest diversity (four species each), followed by Marais de Saint-Laurent-de-la-Prée (three species). Marais de la Vacherie hosts only one species, while no species were detected in Marais du Transbordeur.

Discussion :

The results of this study reveal several key findings regarding bivalve communities in freshwater marshes. The bivalve community appears relatively impoverished, with only seven species detected across five marshes. Additionally, invasive exotic species are present at all sites, except for Marais du Transbordeur, where no species are detected. This highlights a concerning trend of invasive species proliferation in ecosystems, a phenomenon well-documented in other wetlands (STRAYER, 2010; GALLARDO *et al.*, 2016). The detection of *Mytilopsis leucophaeata* (CONRAD, 1831) is notable: an introduced species that, while not yet invasive, has limited data available in France, with only a few known sites (Prié, personal communication, 2024). This raises important questions regarding the future potential for its spread and ecological impacts in French marshes.

Sinanodonta woodiana (I. Lea, 1834), an invasive species well-established in European wetlands, was detected at 80% of sites in this study. These findings suggest that *Sinanodonta woodiana* has successfully colonized these marsh environments and could become a dominant species in the future, as observed in other parts of Europe (ADAM, 2010; KRASZEWSKI & ZDANOWSKI, 2001; CIANFANELLI et al., 2007; LAJTNER & CRNCAN, 2011; PRIE, 2023; TOMOVIC *et al.*, 2013).

The native river mussel *Anodonta anatina* (Linnaeus, 1758), which is absent from Marais de Saint-Laurent-de-la-Prée despite observations of live individuals during dredging operations, highlights another potential discrepancy in the study's sampling method. *Anodonta anatina* is not detected in this marsh due to the limitations of the sampling design. PRIE *et al*. (2023) demonstrate that the detection probability for species like *Anodonta anatina* increases significantly when multiple replicates are performed at each site, emphasizing the need for more extensive sampling to accurately assess species distribution. In this study, only one replicate was performed at each site, likely reducing the chances of detecting less abundant or more cryptic species.

Moreover, the study's limitations, including sampling in stagnant water, which is known to reduce eDNA detection probability (FICETOLA *et al*., 2008), and the turbid water conditions (HOLMES, *et al,* 2024), further compromised the quality of the results. These environmental factors, in addition to the reduced pumping speed to prevent filter clogging, may have affected the quantity and quality of the eDNA samples collected. It is clear that the current results are likely not complete, and further research with optimized protocols is needed to improve the reliability of eDNA-based biodiversity assessments in agricultural freshwater marsh environments.

To improve future studies, we propose modifying the sampling protocol by including hydraulic structures within the marshes, such as sluices and gates. By generating water movement through these structures, the resuspension of eDNA would be facilitated, increasing the likelihood of detecting species that are otherwise difficult to capture in stagnant waters. Additionally, such a technique would be particularly useful during periods of low water levels when a packraft cannot be used for sampling. In these conditions, eDNA is often more concentrated due to reduced water volume, making its detection more efficient if properly resuspended.

To conclude, the detection of invasive species across all the studied sites, along with the observed low diversity of bivalves, reflects the significant anthropogenic pressures faced by these marshes. The influence of human activities, such as water management, habitat alteration, and pollution, is well-documented as a key factor shaping wetland ecosystems and impacting biodiversity (XIONG et al., 2023). Despite these limitations, this study provides valuable baseline data for the conservation and management of bivalve species within these ecosystems. It highlights the need for continuous monitoring, particularly of invasive species, and emphasizes the importance of adopting advanced and optimized sampling techniques in future research.

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Notes on and descriptions of Peruvian Orthalicoidea (Gastropoda, Eupulmonata)

Abraham S.H. BREURE[1,2,3*], Valentín MOGOLLÓN ÁVILA[4]

1 Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium. 2 Natural History Museum, London SW7 5BD, United Kingdom. 3 Naturalis Biodiversity Center, P.O.Box 9517, NL-2300 RA Leiden, the Netherlands (ashbreure@pm.me) ORCID 0000-0001-9357-0501.
*Corresponding author.
4 Universidad Nacional Federico Villarreal, Facultad de Oceanografía, Pesquería, Ciencias Alimentarias y Acuicultura, Roma 350, Lima 18, Perú (svalentinma@yahoo.com) ORCID 0000-0001-5138-5842.

Abstract - Recently collected material from Peru belonging to different families in the superfamily Orthalicoidea (Bulimulidae, Megaspiridae, Orthalicidae) is reported with new localities or being described as new to science. It concerns species belonging to the genera *Bulimulus*, *Naesiotus*, *Quechua*, and *Thaumastus*. *Bostryx beatimorum* Breure, *Bostryx simoni* Breure & Mogollón, *Bostryx vinchosensis* Breure & Mogollón, *Naesiotus gracemontalvanae* Mogollón & Breure, *Suniellus coronensis* Breure & Mogollón, and *Thaumastus* (*Thaumastiella*) *chalamarcaensis* Breure & Mogollón are newly described. *Bulimulus* (*Scutalus*) *punctilineatus* Haas, 1951 is now considered a true *Bulimulus* species based on evidence of the protoconch sculpture.

Key words - *Bostryx*, Bulimulidae, *Bulimulus*, Megaspiridae, *Naesiotus*, Orthalicidae, Orthalicoidea, *Quechua*, *Suniellus, Thaumastus,* new species.

https://zoobank.org/References/8796234E-5469-4D3A-8D3A-4B3515618A3B

Introduction

The superfamily Orthalicoidea is a dominant element in the malacofauna of Peru (RAMÍREZ et al., 2003; BREURE & MOGOLLÓN ÁVILA, 2010). Recently one of us [VMA] made some collections during study trips to different part of Peru and brought some material back belonging to this superfamily, that provides new localities for extant species, plus material we could not identify to any of the known species. Therefore we describe six new species from this material. During study of type specimens we noticed that a species described by Haas needs a different classification, for which we provide evidence.

Material and methods

Part of the specimens collected by the last author (VMA) have been kept in his collection and measured with Vernier callipers with an accuracy of 0.1 mm. One shell of each species was photographed by him. Type material has been deposited in the collection of Museo de la Universidad Federico Villareal, Lima, Peru (MUFV), the Florida Museum of Natural History, Gainesville, U.S.A. (UF), and in the collection of the last author (VMA). The material from Haas is in the collection of the Field Museum of Natural History in Chicago, U.S.A. (FMNH). Other abbreviations used: D, shell diameter; H, shell height; HA, height of aperture; LW, height of last whorl; W, number of whorls; WA, width of aperture. The way the measurements were taken is shown in Figs 1-2.

Systematics

Family Bulimulidae Tryon, 1867

TRYON 1867: 164, 166.

Genus *Bostryx* Troschel, 1847

Bulimus (*Bostryx*) TROSCHEL 1847: 49. Type species by monotypy: *Bulimus* (*Bostryx*) *solutus* Troschel, 1847.

Bostryx beatimorum Breure new species

https://zoobank.org/NomenclaturalActs/f5888875-23c4-4de9-9270-475838f5cf9e

Figs 3–6, Table 1

Description. Shell up to 30. 3 mm, 1.96 times as long as wide, elongate-conical, rather thin; perforate. Sculptured with incrassate growth-lines, lustreless. Protoconch densely coverde with microscopic punctations. Colour whitish to yellowish with axial streaks of beige to dark brown at irregular distances. Whorls 8.1, hardly convex, the last one somewhat swollen, 0.7 the total height, spire with straight sides; suture well impressed. Aperture ovate, 1.27 times as long as wide, 0.45 times total length. Peristome thin and simple.
Type locality and material. Peru, Dept. Ancash, Catzcal, 1010–1189 m, V. Mogollón leg. 17-ii -2016. Holotype MUFV-INV-126; paratypes MUFV-INV-127 (6), VMA 1709 (6).
Animal. The colour of the animal is light brown, with the nerves in the tentacles showing through as dark brown.
Etymology. Named after B. Landoni and T.S. Breure.
Comparisons. This new species, hitherto only known from the type locality, resembles *Bostryx limensis* (Reeve, 1849), but that species is much smaller (18.3 vs 30.3 mm) and is darker coloured with the axial streaks smaller and denser. From *Bostryx modestus* (Broderip, 1832) this novelty differs by being somewhat smaller (30.3 vs 31.6 mm), having a less strong sculpture, and a distinct colour pattern with axial streaks at irregular distances. Finally, this new species may be compared to *Bostryx philippi* (Pfeiffer, 1842), from which it differs by being larger (30.3 vs 24.3), the less swollen last whorl, and the more rimate perforation.
Remarks. Contrary to Ramírez (2004) and Breure & Ablett (2014), *Bostryx limensis* is considered as a valid species due to the different colour pattern and the smaller size compared to *Bostryx modestus* (Broderip, 1832) with which it was placed in its synonymy by Ramírez (2004). The same applies to *Bostryx philippi* (Pfeiffer, 1842), which was considered a synonym of *Bostryx modestus* (Broderip, 1832) by Richardson (1995), but is considered by us as a valid species.

Commenté [F1]: name unavailable, at least not available from that source

Bostryx hamiltoni (Reeve, 1849)

Figs 7–10

Remarks. This species was collected in Peru, Dept. Puno, Puno, Cerro Huajsapata, 3880-3920 m, V. Mogollón leg. 9-xii-2017 (UF 583742 (1), VMA 1715 (6). Living snails that were photographed allow us to describe the external morphology of the animals.
Animal. Colour beige, becoming reddish-brown in the neck, the tentacles becoming darker towards the tips.

Bostryx simoni Breure & Mogollón new species

Figs 11–17, Table 2

https://zoobank.org/NomenclaturalActs/db9206d0-c801-4aeb-9e7f-90515751cdbd

Description. Shell up to 11.5 mm, 1.87 times as long as wide, elongate-conical, thin; rimate. Sculptured with incrassate growth-lines, lustreless. Protoconch almost smooth, with microscopic small punctuations. Colour yellowish with axial streaks of beige to dark reddish-brown at irregular distances and overlaid with broadened, whitish incrassate growth striae; apex gold-coloured, followed by a zone which is dark-blue. Whorls 5.5, hardly convex, the last one somewhat swollen, 0.7 the total height, spire with straight sides; suture well impressed. Aperture ovate, 1.27 times as long as wide, 0.45 times total length. Peristome thin and simple.
Type locality and material. Peru, Dept. Puno, Puno, Cerro Huajsapata, 3889 m, E. Macedo leg. 7-ix-2024. Holotype MUFV-INV-128; paratypes MUFV-INV-129 (4), VMA 1710 (5).
Animal. The colour of the animal is light brown, with the nerves in the tentacles showing through as dark brown.
Etymology. Named after Simon Moldrickx (Amsterdam, the Netherlands).
Comparisons. This mixed coloured species (from top to aperture respectively gold, dark-blue, reddish-brown and yellowish, overlaid with an irregular pattern of whitish axial streaks) is completely different from any other in this region.
Remarks. We were quite surprised to find this species in an urban area, which is in a region considered as rather well-collected. So far this species is only known from the type locality.

Bostryx vinchosensis Breure & Mogollón new species

https://zoobank.org/NomenclaturalActs/0385682a-5774-4ec5-9082-c5dfc84d7ccb

Figs 18–21, Table 3

Description. Shell up to 18.1 mm, 2.04 times as long as wide, elongate-conical, thin; rimate. Sculptured with incrassate growth-lines, and traces of spiral impressions, which result in an irregular, uneven surface; rather shining. Protoconch almost smooth, with microscopic small punctuations. Colour horny brown, with axial streaks of whitish, in the last two whorls with dispersed, small spots showing the ground colour, which becomes more reddish-brown towards the peristome. Whorls 6.8, hardly convex, the last one somewhat swollen, 0.72 the total height, spire with straight sides; suture well impressed. Aperture elongate-ovate, 1.57 times as long as wide, 0.46 times total length. Peristome thin and simple.

Type locality and material. Peru, Dept. Junín, Prov. Jauja, Canchayllo, Quebrada Vinchos, 3783 m, V. Mogollón leg. 23-vi-2017. Holotype MUFV-INV-130; paratypes MUFV-INV- 131 (3), VMA 1711 (2).

Etymology. Named after the type locality.

Comparisons. This new species may be compared to *Bostryx balsanus* (Morelet, 1863), from which it differs by the different colour pattern, the less swollen last whorl, and the rimate perforation. It may also be compared to *Bostryx ferrugineus* (Reeve, 1849), which has a more swollen last whorl, a different shaped aperture, and a broader perforation. The colour pattern of this novelty resembles *Bostryx hennahi* (Gray, 1828), but that species is larger (24.4 vs. 18.2 mm), has a relatively smaller aperture, and a broader perforation.

Bostryx vittatus (Broderip, 1832)

Figs 22–33

Remarks. This species was described by Broderip in Broderip & Sowerby (1832: 31) as *Bulinus vittatus*, with type locality “Peruviâ (Ilo)“.

Breure (1978: 140) wrote: “Pilsbry (1896: 156) has suppressed *Bulinus vittatus* Broderip in favour of *Buliminus styliger* Beck, 1837, on account of the existence of *Bulimus vittatus* Spix, 1827. *Bulimus* as used by Spix referred to *Bulimus* Scopoli, 1777 (proposed for lymnaeid and succineid species). *Bulinus* as used by Broderip referred to *Bulinus* Studer, 1820 (not *Bulinus* Müller, 1781), an entirely different taxon, proposed for enid species. Pilsbry's nomenclatural approach was probably not in line with present-day nomenclatural rules. [This is currently in ICZN (2024): Article 56.2]. *Bulimus styliger* Beck, 1837, is thus a junior synonym of *Bulinus vittatus* Broderip, 1832“. This was not followed by Richardson (1995: 46–47) who mentioned Broderip’s taxon as synonym of *Bostryx styliger* (Beck, 1837). However, the correct name of Broderip’s taxon is *Bostryx vittatus* (Broderip, 1832).

In Zamaca (also written as Samaca), ruins near the mouth of the Río Ica, the second author received from archaeologist Manuel Gorriti, a series of shells of which some (Figs 22–25) strongly resemble this species and which we tentatively identify as such. The series show an interesting transition to carinated forms of which some (Figs 28–29) are similarly shaped as *Bostryx reentsi* (Philippi, 1851) (see Breure 2008: fig. 13), while others (Fig. 33) resemble transition forms of *Bostryx multiconspectus* Breure, 2008 between elongate and depressed shells. A field study of the latter species suggested that this transition may be induced by ecological factors and should be considered as morphological continuum (Breure et al. 2024). Elsewhere, Johnson et al. (2016) and Johnson & Stankowski (2018) reported on similar cases from Western Australia.

Genus *Bulimulus* Leach, 1814

Bulimulus Leach 1814: 41. Type species by subsequent designation (Pilsbry 1896 [1895–1896]: 125) *Bulimulus trifasciatus* Leach, 1814.

Bulimulus punctilineatus Haas, 1951

Figs 34–35

Remarks. This species was originally described as *Bulimulus* (*Scutalus*) *punctilineatus* by Haas (1951: 517) from Peru, Urubamba valley, Sahuayaco, 800 m. Breure (1979: 57) treated this species as a *Bostryx*, while Richardson (1995: 356) classified it under *Scutalus* Albers, 1850. During preparation of a revision of *Bostryx* species from Peru we downloaded the images of the holotype deposited as FMNH 30914. We noticed that the sculpture of the protoconch was different than those normally seen in *Bostryx*, and also seemed different than the sculpture known from *Scutalus* species. After having received detailed images of the protoconch (Fig. 35), which shows the characteristic sculpture of this genus, it appeared that this taxon has to be considered as a true member of *Bulimulus* Leach, 1814.

Bulimulus tyleri Dall, 1912

Figs 36–41

Remarks. Dall (1912: 6) introduced this name as a replacement name for *Bulimus simplex* Hupé, 1857 not Jonas, 1843. For some time this species was placed in *Bostryx* (Breure 1979, Richardson 1995, MolluscaBase 2024). However, recent inspection of the protoconch convinced us that the generic classification by Dall is correct. The protoconch sculpture is totally unlike that in *Bostryx*, but confirms the sculpture found in *Bulimulus* (Breure, 1974; 1978). The type material is MNHN-IM-2000-28112 (Figs 36–38). The specimen that Dall used for his study (USNM 250261; Figs 39–41), however, does not look like this material.

Commenté [F2]: citation "see Breure..." would avoid misinterpretations, Breure is not the author of Bulimulus.

Genus *Naesiotus* Albers, 1850

Naesiotus Albers 1850: 162. Type species by subsequent designation (Albers & Von Martens 1860: 220) *Bulinus nux* Broderip, 1832.

Remarks. The type species of this genus occurs on the Galápagos Archipelago and the relationship between the *Naesiotus* species on this island group and those on the mainland is still unknown (C. Parent, in litt.). Also the relationship with the group of *Protoglyptus* Pilsbry, 1897 from the Caribbean and *Rabdotus* Albers, 1850 from Mexico and the U.S.A. remains so far enigmatic. We hope that future molecular research will shed light on this taxonomic puzzle. For now, we prefer to use *Naesiotus* for the Peruvian species.

Naesiotus bambamarcaensis Weyrauch, 1960

Figs 42–44

Remarks. This species was described by Weyrauch (1960: 37) from Dept. Cajamarca, Río Llaucán, Cerro Machaipungo, 4 km NW Bambamarca, 3000 m. A new localities is in the same department, Chota Province, Chalamarca District, Centro Poblado Mayor El Verde, El Pedregal, 2896 m; this is circa 20 km N Bambamarca (UF 583734 (2); VMA 1716 (2)).

Naesiotus gracemontalvanae Mogollón & Breure new species

https://zoobank.org/NomenclaturalActs/68c24237-7435-442b-a5bd-3b92cf7e8e3e

Figs 45–50, Table 4

Description. Shell up to 13.2 mm, 2.27 times as long as wide, elongate-conical, rather thin; rimate. Sculptured with relatively small axial granules, arranged in spiral rows and covered by an irregular pattern of candle wax-like whitish, which leave the ground colour visible especially on the last two whorls. Protoconch sculptured with axial riblets with excessive fine spiral lines in between; the interstices are circa 5 times the width of the riblets. Ground colour (dark-)reddish. Whorls up to 7.7, somewhat convex, the last one 0.6 the total length, spire with straight sides; suture well impressed. Aperture 1.6 times as long as wide, 0.37 the total height, truncated-oblong, the length axis deviating from the shell axis. Peristome thin, the columellar margin reflected and triangular, parietal callus transparent.
Type locality and material. Peru, Dept. Cajamarca, Chota Province, Chalamarca District, Centro Poblado Mayor El Verde, Cerro Las Viejas, 3150 m, V. Mogollón leg. 21-ii-2018. Holotype UF 583748, paratypes MUFV-INV-132 (4, dry), UF 583735 (7, dry), VMA 1712 (4, dry).
Animal. The body is dark-brown to blackish-brown.
Etymology. Named after our collaborator Grace Montalván Naranjos from the Universidad Nacional Federico Villareal (Lima).
Comparisons. This new species, known hitherto from the type locality only, resembles *Naesiotus cerrateae* Weyrauch, 1967, from which it differs by having the ground colour reddish with an irregular pattern of whitish, less slender (H/D 2.23 vs 2.77), and a relatively larger last whorl (0.60 vs 0.49). From *Naesiotus subcostatus* (Haas, 1948) this new species differs in its colour pattern, the sculpture of the shell, and the more swollen last whorl. Finally it may be compared to *Naesiotus gracillimus* Weyrauch, 1956, from which it differs in its stouter shape (H/D 2.45 vs 2.23), the different sculpture, and the different colour pattern.

Genus *Suniellus* Breure, 1978
Scutalus (*Suniellus*) Breure 1978: 188. Type species by original designation *Scutalus* (*Suniellus*) *chillu* Breure, 1978.
Remarks. This genus is now considered as the high-altitude sister-group of *Kuschelenia* Hylton Scott, 1951. Four species are hitherto known, occurring in Bolivia, Peru, Ecuador and Colombia (Breure 2011).

***Suniellus coronensis* Breure & Mogollón new species**
https://zoobank.org/NomenclaturalActs/e7e03719-fdbe-4eec-809a-3f56c8c055af

Figs 51–58, Table 5

Description. Shell up to 35.7 mm, 1.75 times as long as wide, elongate, rather thin; imperforate. Sculptured with irregularly spaced, thickened growth-striae, in between with weaker incrassations, and spiral rows of oblong granules, especially on the last two whorls. Protoconch sculptured with axial wrinkles on upper part of the whorl, becoming short granules in different directions on the lower part. Colour yellowish-olivaceus with brownish, axial streaks, especially on the last whorls, becoming dark brown to blackish-brown towards the lip; on the third and fourth whorl a whitish lattice turning into a violet-coloured apex. Whorls 7, somewhat convex, the last one swollen, 0.80 the total length, spire with straight sides; suture well impressed. Aperture 1.36 times as long as wide, 0.54 the total height, inverse ear-shaped, the length axis deviating from the shell axis. Peristome thin, the columellar margin broadly triangular and reflected over the closed umbilicus, parietal callus whitish.
Type locality and material. Peru, Dept. Cajamarca, Hualgayoc Province, Hualgayoc District, Cerro Corona, 3958 m, V. Mogollón leg. 19-ii-2018. Holotype UF 583749, paratypes UF 583736 (1 dry), UF 583740 (1 wet), paratypes VMA 1713 (1 dry).
Etymology. Named after the type locality (Fig. 58).
Comparisons. This new species resembles *Suniellus troscheli* (Philippi, 1867), so far the only other congeneric species in Peru, but differs in the colour pattern, the sculpture of the shell, and the ear-shaped aperture.

Family Orthalicidae Martens, 1860
Martens in Albers & Martens, 1860: 209.

Genus *Quechua* Strebel, 1910
Thaumastus (*Quechua*) Strebel 1910: 17. Type species by monotypy: *Bulimus salteri* G.B. Sowerby III, 1890.

***Quechua salteri* (G.B. Sowerby III, 1890)**
Figs 56–62

Remarks. This species was described by Sowerby III (1890: 578) from "Catamarca, Andes Peruviae" and mentioned from "Dept. Cajamarca, Chota" by Breure & Mogollón (2016: 63). We can now provide a detailed locality from the same department, Chota Province, Chalamarca District, Centro Poblado Mayor El Verde, Cerro Sugarorco, 2989–3052 m, V. Mogollón leg. 21-ii-2018 (UF 583738 (2), UF 583739 (1), VMA 1717 (1). Several specimens were collected, among which were living ones (Fig. 59). The animal has a whitish body with relatively large, oblong tubercles, a blackish neck, and a bright yellowish zone at the rim of the foot.

Family Megaspiridae Pilsbry, 1904
Pilsbry 1904 [1903–1904]: 175.

Remarks. In a recent phylogenetic study of the Orthalicoidea (Salvador *et a*l. 2023) the Megaspiridae appeared as a non-monophyletic group. Future studies should resolve its position.

Genus *Thaumastus* E. Martens, 1860
Thaumastus Martens in Albers & Martens 1860: 215. Type by original designation *Bulimus hartwegi (*Pfeiffer, 1846).

Commenté [F3]: Should read Thaumastus Albers, 1860. The name was ascribed to Albers in that work, where Martens explained in the introduction that until 1857 Albers worked on the manuscript, and after 1857 Martens alone worked on the manuscript. So this was a joint work with content compiled by both authors Albers and Martens. Art. 50.1 (not 50.1.1) should be applied here.
It is unclear why MolluscaBase ascribes inconsistently some names of that 1860 work to Albers and others to Martens. Even if Martens is regarded as an editor of content compiled by Albers (as explained on the Thaumastus page in MolluscaBase, version 24 Nov 2020), the name should be attributed to Albers, because a name is attributed to an author and not to an editor.

***Thaumastus* (*Thaumastus*) *sumaqwayqu* Breure & Mogollón, 2016**
Remarks. A new locality for this species is Dept. Cuzco, Prov. La Convención, Quillabamba, between Chaupimayo and Lanascayoc, Montaña Madre Selva, 1715 m, V. Castillo leg., v-2023, VMA 1718 (8).

Subgenus *Thaumastus* () Weyrauch, 1956

Thaumastus (*Thaumastiella*) Weyrauch 1956: 11. Type species by original designation *Bulimulus sarcochrous* Pilsbry, 1897.

Thaumastus (*Thaumastiella*) *chalamarcaensis* Breure & Mogollón new species

https://zoobank.org/NomenclaturalActs/3b950a66-354b-4385-add1-56572cdd41f0

Figs 60–64, Table 6

Description. Shell up to 47.2 mm, 1.97 times as long as wide, elongate, rather solid; rimate. Sculptured with irregularly spaced, thickened growth-striae, in between with weaker incrassate striae, and spiral rows of oblong granules, especially on the upper part of the last two whorls. Protoconch sculptured with axial riblets, which become wavy, anastomosing and irregularly broken up into bead-like to oblong granules on the second whorl. Towards the transition to the teleoconch the granules become more densely spaced. Colour pinkish-violet with brownish, axial streaks, intermingled with yellowish in an irregular pattern, overlaying the brown, especially on the last whorls. A dark yellow-browish girdle at the periphery underneath the light yellow axial streaks. Whorls 5.5, somewhat convex, the last one 0.57 the total length, spire with straight sides; suture well impressed and slightly crenulate. Aperture 1.37 times as long as wide, 0.50 the total height, inverse ear-shaped, the length axis slightly deviating from the shell axis. Peristome thin, pink-violet, the columellar margin broadly triangular and reflected over the narrow umbilicus, columella with a convexity at the transition to the parietal wall, parietal callus with a pink-violet hue, transparent.
Type locality and material. Peru, Dept. Cajamarca, Chota Province, Chalamarca District, Centro Poblado Mayor El Verde, Cerro Sugarorco, 2989–3052 m, V. Mogollón leg. 20-ii-2018. Holotype UF 583750. Paratypes UF 583737 (2, dry), UF 583745–7 (4, wet), MUFV-INV-133 (4, dry), VMA 1714 (4 dry). Additional no type material VMA 1719 (20, wet).
Animal. The body of the snail is greyish-blue (Fig. 67).
Etymology. Named after the district in which the type locality lies.
Comparisons. This new species resembles *Thaumastus* (*Thaumastiella*) *occidentalis* Weyrauch, 1960, which occurs ca. 100 km SSW of the type locality. This novelty differs from that species by a more densely granulated transition zone between the protoconch and the teleoconch, having an ear-shaped aperture, and a convexity in the columella. In the new species the colour patterns also differs with having irregular yellow longitudinal streaks and a pink-violet parietal callus, as well as the inside of the aperture.

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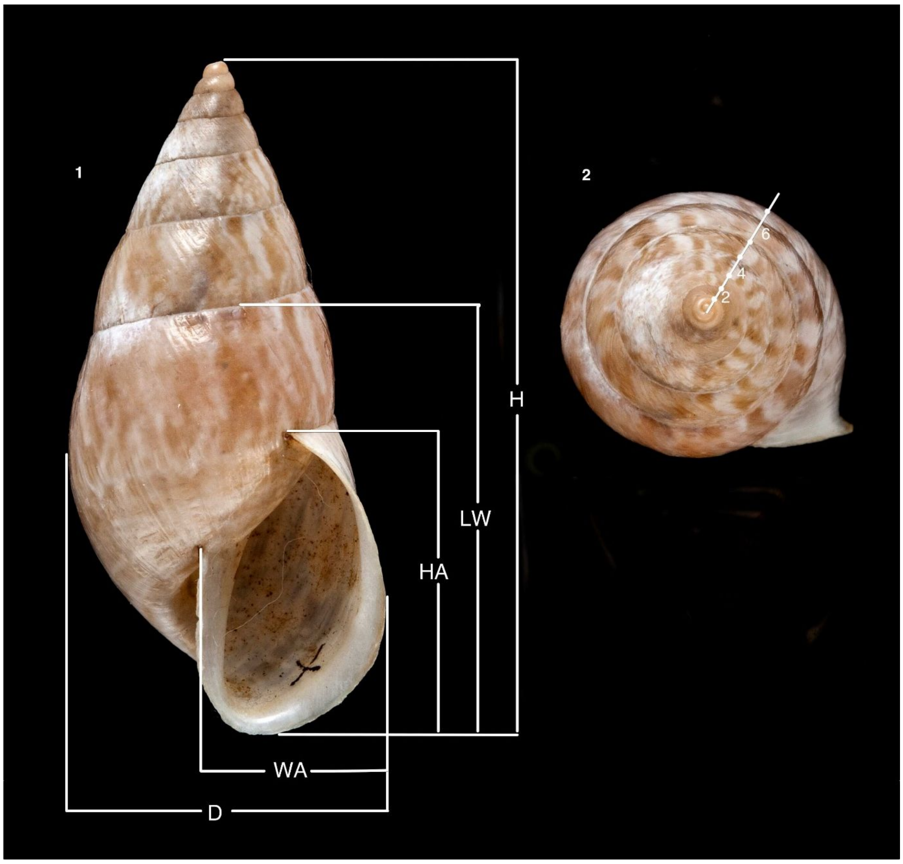
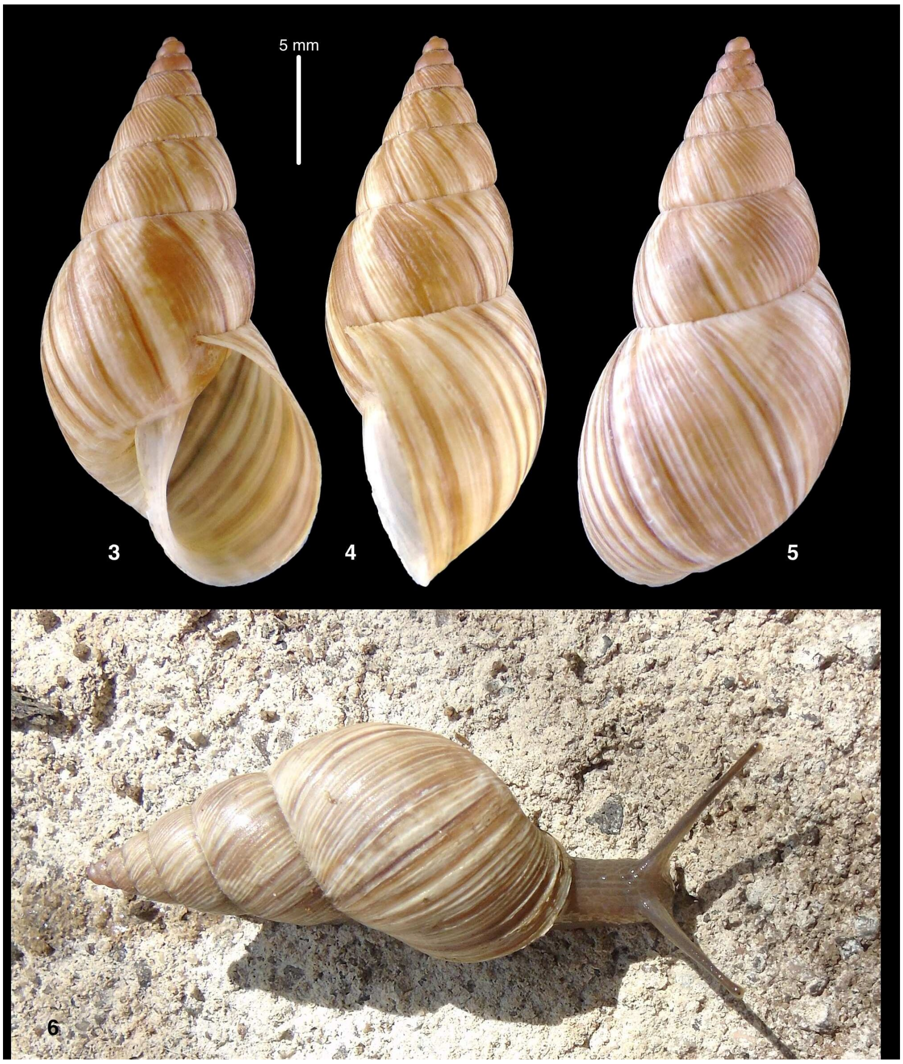
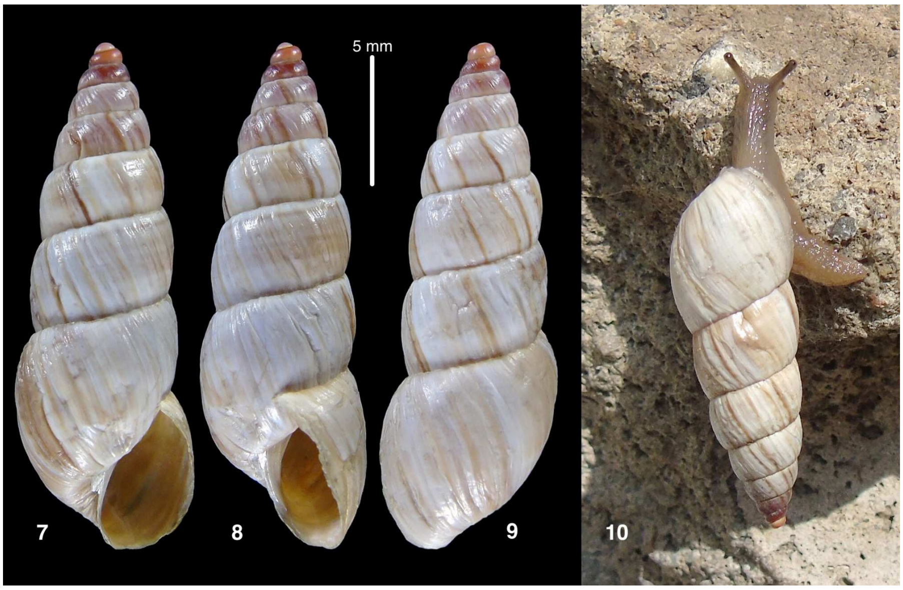

1
2
H
LW
HA
WA
D
2
4
6

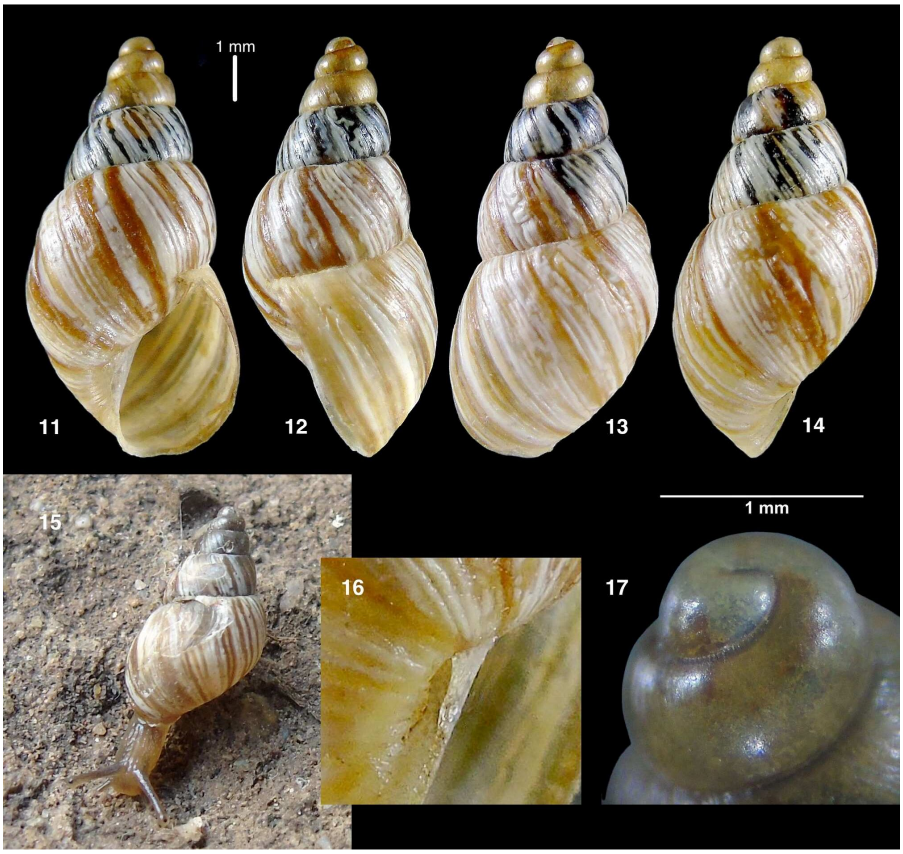
Figs 1–2. Measurements of the shell. 1, Length and width measurements. 2, Whorl measurements.



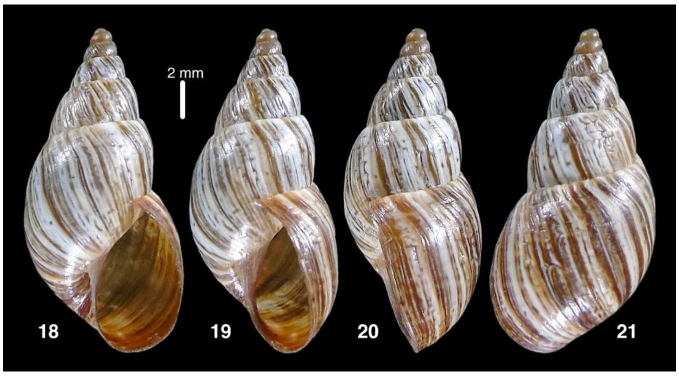
Figs 3–6. *Bostryx beatimorum* Breure n.sp. 3–5. Different views of holotype. 6. Living specimen at type locality.



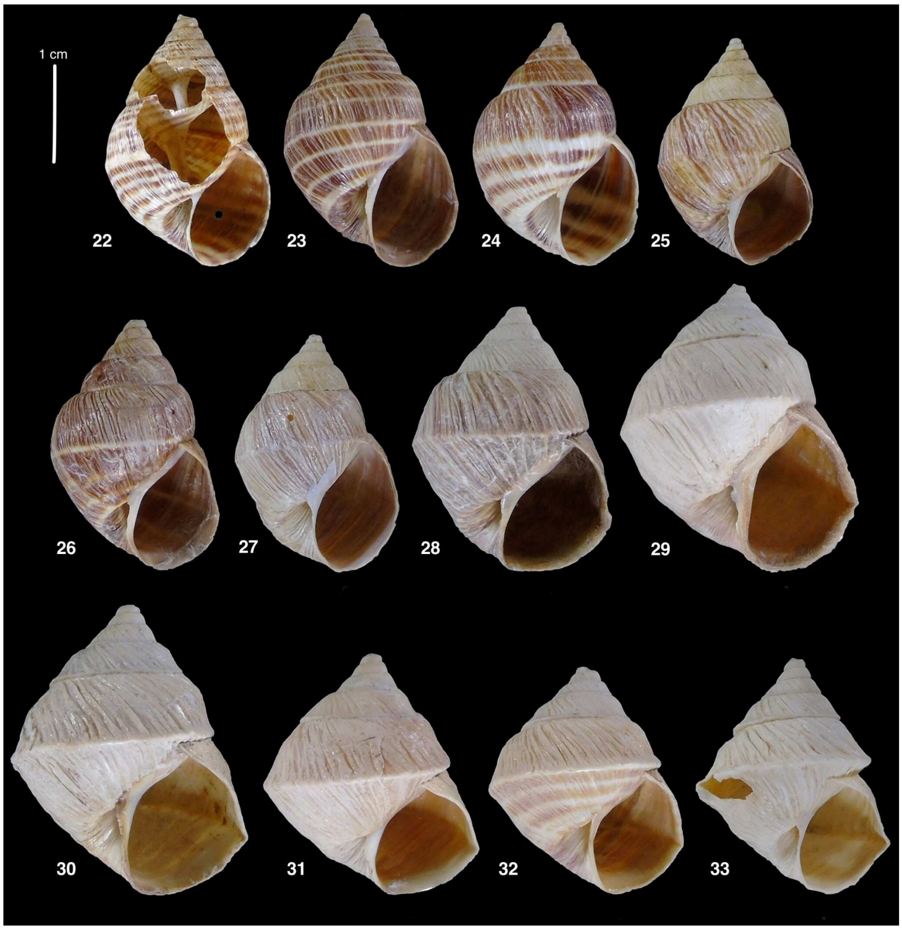
Figures 7–10. *Bostryx hamiltoni* (Reeve, 1849). Cerro Huajsapata, Puno.


1 mm
11
12
13
14
15
1 mm
16
17

Figs 11–17. *Bostryx simoni* Breure n.sp. 11–14. Different views of holotype. 15. Living specimen at type locality. 16. Detail of shell showing perforation. 17. Protoconch.


2 mm
18
19
20
21

Figures 18–21. *Bostryx vinchosensis* Breure & Mogollón n.sp., holotype. Quebrada Vinchos, Junin.


1 cm
22
23
24
25
26
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29
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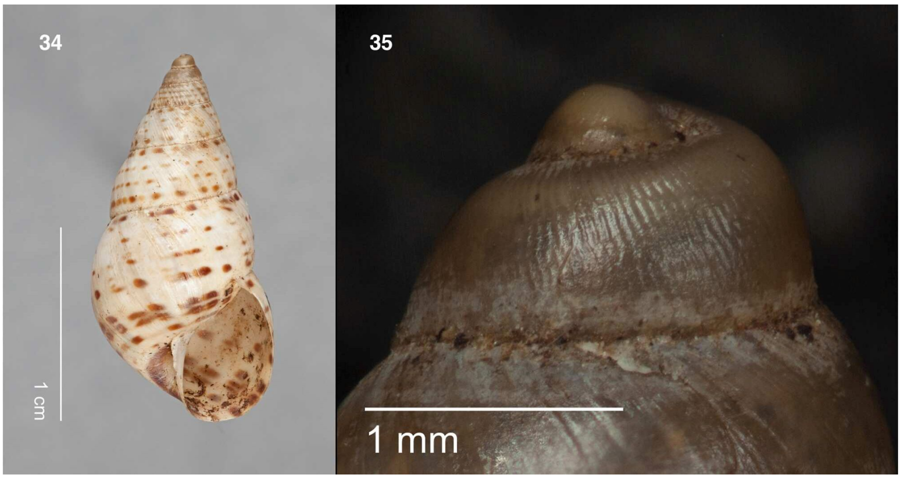
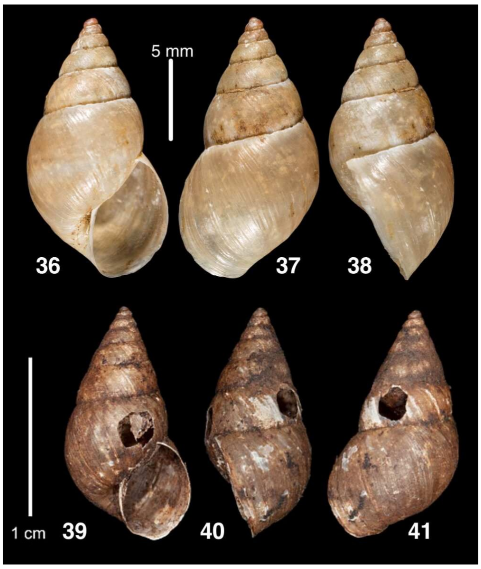
31
32
33

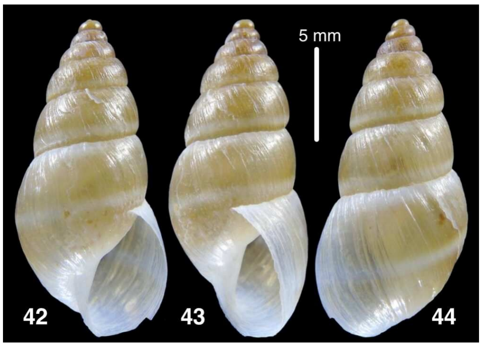
Figs 22–33. *Bostryx vittatus* (Broderip, 1832). Transition series from Samaca, Ica.



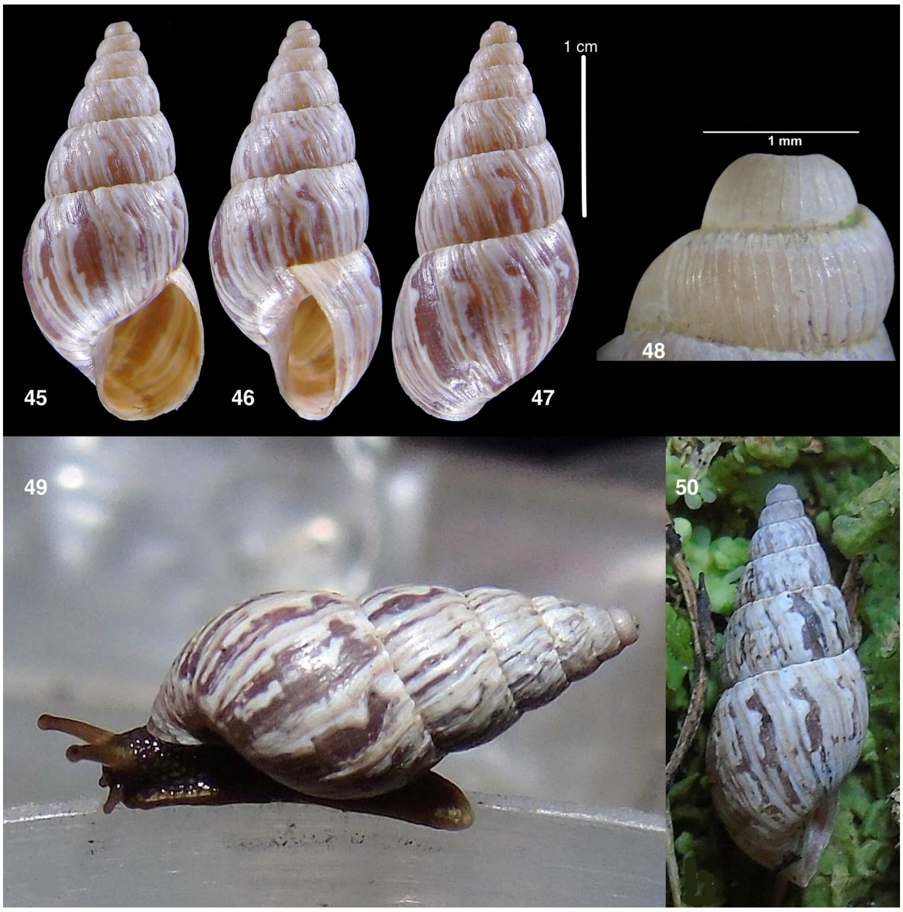
Figs 34–35. *Bulimulus punctilineatus* F. Haas, 1951. Holotype FMNH 30914, shell and protoconch sculpture.



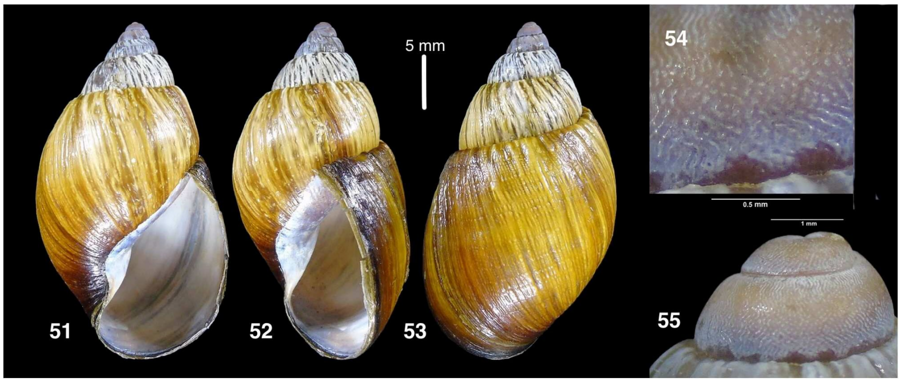
Figs 36–41. *Bulimulus tyleri* Dall, 1912. 36–38, *Bulimus simplex* Hupé, 1857, lectotype MNHN-IM-2000-28112. 39–41, *Bulimulus* (*Scutalus*) *tyleri* Dall, 1912, “holotype” [sic] USNM 250261.



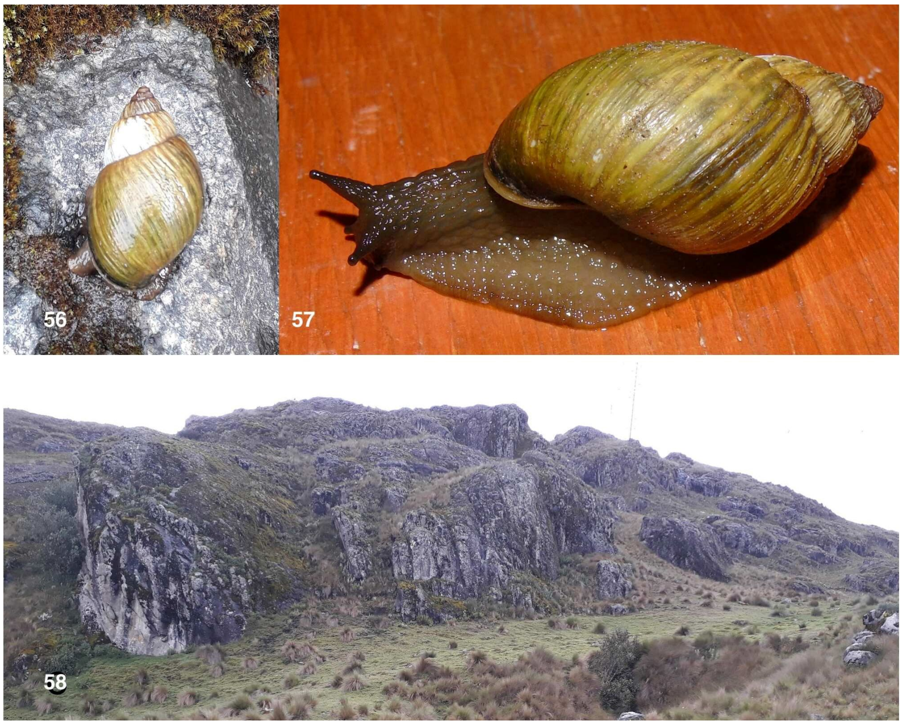
Figs 42–44. *Naesiotus bambamarcaensis* Weyrauch, 1960. Peru, Cajamarca, El Verde.


1 cm
1 mm
45
46
47
48
49
50

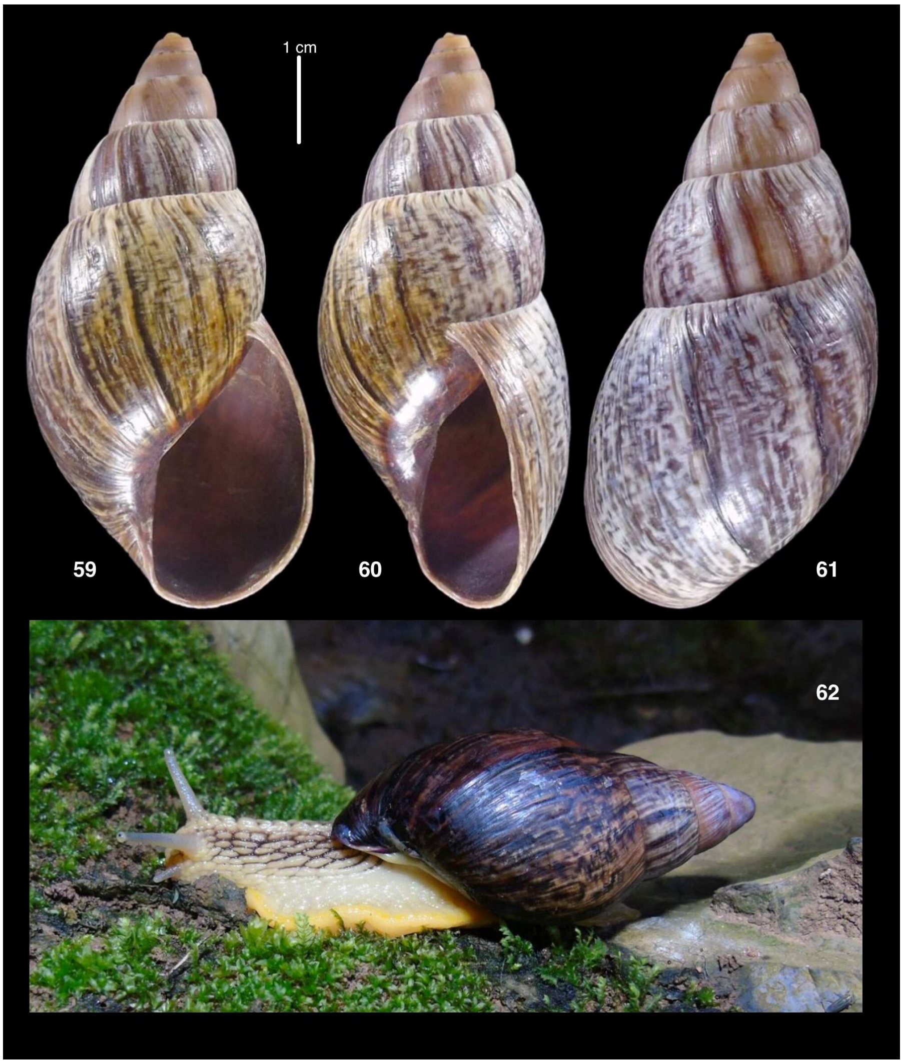
Figs 45–50. *Naesiotus gracemontalvanae* Mogollón & Breure n.sp. 45–47. Different views of holotype. 48. Protoconch sculpture. 49–50. Living specimen at type locality.


5 mm
54
0.5 mm
1 mm
55
51
52
53

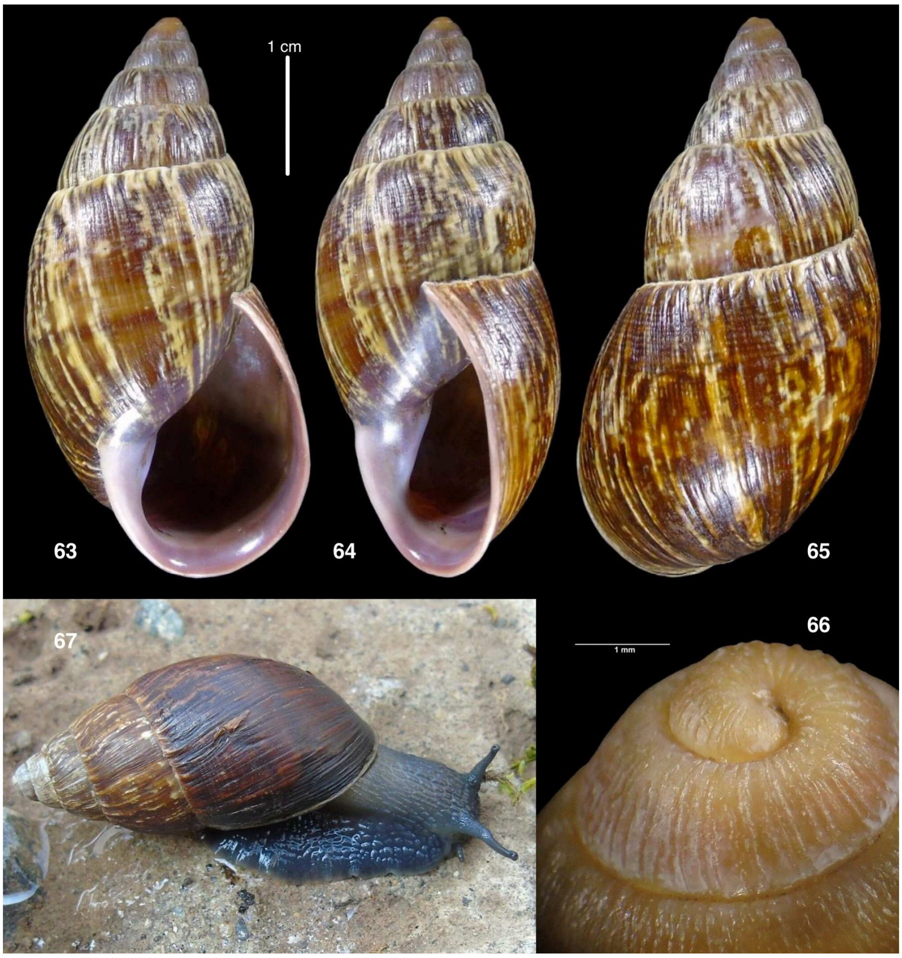
Figs 51–55. *Suniellus coronensis* Breure & Mogollón n.sp. 51–53. Different views of holotype. 54–55. Protoconch sculpture.



Figs 56–58. *Suniellus coronensis* Breure & Mogollón n.sp. 56–57. Living specimen. 58. Habitat at type locality.



Figs 59–62. *Quechua salteri* (G.B. Sowerby III, 1890). 59–61. Cerro Sugarorco, Cajamarca. 62. Living specimen.



Figs 63–67. *Thaumastus* (*Thaumastiella*) *chalamarcaensis* Breure & Mogollón n.sp. Cerro Sugarorco, Cajamarca. 63–65. Different view of holotype. 66. Protoconch sculpture. 67. Living specimen at type locality.

Table 1. Measurements in *Bostryx beatimorum* Breure n.sp.

Table 1 - Measurement in *Bostryx beatimorum*

	H	D	HA	WA	LW	W
Holotype MLP	28.4	13.4	13	7.1	18.6	8.1
Paratypes MLP	30.3	13.7	13.7	6.7	19.1	8.4
	29.7	14.2	12.3	7	19	8.5
	25.3	13.2	12.1	6.5	17.5	7.6
	27.1	13.3	12.5	7	17.2	7.9
	26.1	13.2	12.7	6.6	18.3	7.6
	29.1	13.1	13	6.3	19	8.2
Paratypes VMA 1709/6	28.8	14.2	13.3	6.4	18.5	8.1
	26.2	13.2	11.6	6.1	16.9	8.1
	29.4	14.9	14.2	7.1	19.9	8
	28	13.6	12.7	6	18.3	7.9
	26.4	12.5	11.4	5.6	17	8
	27	13.9	12.3	6.3	17.5	8

Table 2. Measurements in *Bostryx simoni* Breure & Mogollón n.sp.

Table 2 - Measurements in *Bostryx simoni*

	H	D	HA	WA	LW	W
Holotype MLP	11.2	5.7	5.3	2.9	8	6.3
Paratypes MLP	10.8	6	5.4	3	7.8	5.8
	11	5.8	5.3	3	7.6	6.1
	9.8	5.2	4.8	2.6	7.1	5.7
	9.7	5.4	5	2.9	7.2	5.7
Paratypes VMA 1710/5	9.1	5	4.9	2.5	6.7	5.7
	9	5	4.8	2.6	6.6	5.5
	9.5	4.9	4.9	2.6	6.8	5.7
	9.2	5	4.7	2.4	6.8	5.7
	10.2	5.5	5	2.9	7.3	5.8

Table 3. Measurements in *Bostryx vinchosensis* Breure & Mogollón n.sp.

Table 3 - Measurements in *Bostryx vinchosensis*

	H	D	HA	WA	LW	W
Holotype MLP	18.1	8.9	8.2	4.4	12.2	6.8
Paratypes MLP	18.9	9.3	8.8	4.8	14	7.2
	17.3	8.5	8.2	4	12	7.1
	13.9	7	7.2	3.6	10.2	6.3
Paratypes VMA 1711/2	17.6	9.4	8.9	4.8	12.5	6.9
	17	8.7	8.4	4.5	11.6	6.8

Table 4. Measurements in *Naesiotus gracemontalvanae* Mogollón & Breure n.sp.

Table 4 - Measurements in *Naesiotus gracemontalvanae*

	H	D	HA	WA	LW	W
Holotype UF	13.0	5.9	5.2	3.1	7.8	7.0
Paratypes UF	12.9	5.5	4.6	2.7	7.4	7.0
	12.0	5.3	4.5	2.9	7.2	7.0
	12.9	5.4	4.9	2.6	7.0	7.1
	12.3	5.4	4.2	2.9	7.1	7.0
	11.6	5.1	4.6	2.9	7.0	6.0
Paratypes MLP	11.2	5.2	4.2	3.1	6.8	5.7
	12.6	5.2	5.1	2.6	7.6	7.5
	12.5	5.4	5.2	2.8	7.7	7.3
	12.9	5.8	5.3	3.1	7.9	7.3
Paratypes VMA 1712/4	12.7	5.9	5.2	3	7.7	7.7
	12.2	5.5	5.1	2.7	7.5	7.5
	13.2	5.9	5.1	3.1	7.8	7.7
	11.2	5.5	4.7	2.8	7.1	7.2
	11.2	5.3	4.7	2.6	7.1	7.1
Mean	12.27	5.4	4.6	2.88	7.18	

Table 5. Maesurements in *Suniellus coronensis* Breure & Mogollón n.sp.

Table 5 - Measurements in *Suniellus coronensis*

	H	D	HA	WA	LW	W
Holotype UF	34.5	19.9	20.4	13.3	27.1	6.2
Paratype UF	35.7	21.3	20.9	13.7	27.7	6.0
Paratype VMA 1713/1	34.6	20.6	20.2	10	27.2	7

Table 6. Measurements in *Thaumastus* (*Thaumastiella*) *chalamarcaensis* Breure & Mogollón n.sp.

Table 6 - Measurements in *Thaumastus chalamarcaensis*

	H	D	HA	WA	LW	W
Holotype UF	47.2	23.4	24.7	17.1	33.7	6.0
Paratypes UF	44.9	19.2	19.2	12.4	31.5	5.8
	42.5	18.5	18.7	11.6	29.2	5.8
Paratypes MLP	43.6	19	20	10.6	31	7.1
	43.4	19.5	20.8	10	31.7	7.3
	42.4	18.7	19.9	10.1	30.1	7.1
	44.1	19.4	20	9.7	30.5	7.4
Paratypes VMA 1714/4	40.4	19.7	20.5	9.7	29.7	7.1
	39.1	19.3	21	10.1	29.3	6.8
	39	19.4	20.7	10.2	29.3	6.7
	40.7	20.9	20.5	10.5	29.4	7.3

Checklist of marine mollusk fauna collected by tangle nets from Daya Bay, Guangdong, China, with descriptions of new species and new combination

Li-Wen LIN[1, 2], Ji-Lin JIANG[3] & Yang SHAO[4]

[1]Xiufeng Road 158 Fengdanbailu 24, Jin'an District, Fuzhou 350012, P. R. China;
*linliwen0911@foxmail.com
[2]Hubei Broad Nature Technology Service Co., Ltd., Wuhan 430079, P.R. China;
[3]NO.13 Road 23, Yingzhou 8th Street, Xiaozhou Village, Haizhu District, Guangzhou 510320, P.R. China;
[4]Art Park of Yinxiang Street NO.209, Xiaobao Village, Songzhuang Town, Tongzhou District, Beijing 101100, P.R. China.

Abstract - A study on small to micro marine mollusks collected by tangle nets from shallow water in Daya Bay, Guangdong, China yielded a result of more than 100 species belonging to 51 families. The species composition of this fauna is compared with those of adjacent areas, especially the fauna of Xiajinwan, Fujian, China. An illustrated checklist of this fauna is provided with 4 new species being described based on conchological characters. The geographical features of Daya Bay and the characteristics of its benthic marine organisms are introduced, and comprehensive researches on marine mollusk fauna of China and neighbouring countries are discussed.

Key words - China, Guangdong, mollusk fauna, new species.

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Introduction

The comprehensive researches on Chinese marine mollusk fauna began in the 1840s, when the Danish malacologist as well as a military doctor, Theodore E. Cantor, landed in Zhoushan [Chusan] Island, Zhejiang, China with the British forces during the First Opium War. (Benson W. H. 1842 & Benson W. H. 1855). Subsequently, a large number of Chinese seashell specimens were transported to Europe and stored in museums for research purposes. During this period, Chinese malacologists such as Teng-Chien Yen, Soh-Chu Gee King and Chi Ping systematically documented the marine mollusk species in certain regions of China (*e.g.* Xiamen [Amoy] of Fujian and Beidaihe [Peitaiho] of Hebei)(Yen 1933, Grabau & King 1928, Chen & Wu 2020). Over the past half-century, many Chinese malacologists conducted meticulous and comprehensive researches on seashells in China, as many fauna monographs or essays were published, including Fauna Sinica series (*e.g.* Zhang 2008, Xu & Zhang 2008, Wang *et al.* 2016). It is worth noting that some of these works focus on small to micro-sized marine mollusks which have been overlooked for a long time due to their size (*e.g.* Zhang 1995, Feng 1996, Chen & Lee 2007, Lin & Rol ά n 2024). In neighbouring countries of China, including Japan, Vietnam and the Philippines, comprehensive studies on marine mollusk fauna are also fruitful (*e.g.* Nguyen 2007, Okutani (ed.) 2017, Poppe 2008–2017), which help a lot for the identification of Chinese marine mollusks.

Daya Bay is a semi-enclosed coastal bay located in the northeastern part of the South China Sea, bordering Huizhou, Guangdong Province, China. It spans approximately 600 square kilometers, with an average depth of 11 meters and a maximum depth of 21 meters near its mouth. The bay features a complex coastline with numerous islands and coves, creating diverse habitats for marine life. Its water temperature is influenced by subtropical monsoon climates as well as partly by the operation of the Daya Bay Nuclear Power Station. The temperatures range from 14.76°C in winter to 29.84°C in summer in the years between 1982 to 1989, and range from 14.00°C in winter to 35.00°C after the operation of the station in 1994–1995 (Wang *et al.* 2004).

Marine environment of Daya Bay supports rich benthic biodiversity, particularly mollusks, crustaceans, and polychaetes. Sediment types vary from sandy to muddy substrates, fostering distinct benthic communities. Seagrass beds and coral patches occur in some areas, enhancing ecological complexity. However, the bay faces degradation of mangroves, red tides and constructions along the coast, which impact water quality and species distribution (Zhang *et al.* 2017). Wang *et al.* 2004 documents 251 marine mollusk species collected in Daya Bay, which mainly focuses on small to large-sized species over 10 mm in length. In this work, small to micro marine mollusks collected by tangle nets from Daya Bay are studied, which not only improves the knowledge of marine mollusks in this area, but also enriches the diversity of micro marine mollusk fauna of China.

Material and methods

Shell materials used in this study were picked up from the tangle nets on the harbour of Daya Bay, Huizhou, Guangdong Province, China. The tangle nets were used in fishing at the depth of 5–10 m in Daya Bay. Anhydrous ethanol was used to clean the shells preliminarily and degreasing cotton with alcohol was used to remove the dirt on the surface of the shells.

Conventional photos of the shells were taken using Mitutoyo M Plan APO 10×/20× objective with a Raynox DCR150 tube lens and Nikon D80 camera with Laowa 60mm F2.8 Macro 2:1 lens. Pictures were modified in Adobe Photoshop CC 2019.

Number of whorls of *Pseudoliotia* Tate, 1898 is calculated after Rubio & Rolán (2018), and that of Conoidean snails is calculated after method E of Van Osselaer (1999). Measurement of shells is described as shell width (diameter)× shell height.

Abbreviations:
ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia, U.S.A.
BMNH: British Museum (Natural History), London, U.K.
MANCH: Manchester Museum, the University of Manchester, Manchester, U.K.
JJL: Collection by Ji-Lin Jiang (Zhaoqing, China).
LLW: Collection by Li-Wen Lin (Fuzhou, China).
MNHN: Muséum national d'Histoire Naturelle, Paris, France.
SCSMBC: Marine biodiversity collections of South China Sea Chinese Academy of Sciences, Guangzhou, China.
SD: Collection of Shasky D.R (California, U.S.A).
SY: Collection by Yang Shao (Beijing, China).

Results

Shells of three classes, Gastropoda, Bivalvia and Scaphopoda are recorded with 51 families and 168 species recognized. The sampling mainly focuses on intact specimens under 20 mm while fragments of larger species are not reckoned in the statistics. The most among these species are typical subtidal zone species or species from deeper water which mainly belong to families Epitoniidae, Zebinidae, Vanikoridae, Vitrinellidae, Mangeliidae, Raphitomidae, Clathurellidae, Pyramidellidae, etc. Some intertidal species such as *Clypeomorus* cf. *pellucida* (Hombron & Jacquinot, 1848) and *Calliostoma spesa* J.-L. Zhang, Wei & S.-P. Zhang, 2018 are also recorded.

A preliminary analysis of the composition of species of above mentioned fauna has been made by comparison of species from other sea areas of China, as well as of Japan, Korea and Southeast Asia, particularly Philippines. The studies result in 4 new species of Gastropoda which are intensively described in this work and one new combination is proposed. A checklist with photographs of small to micro species collected by tangle nets from Daya Bay and abundance of each species is provided, which makes further researches of this fauna available.

Discussion

Influenced by the geographical location of southern China, the mollusks in Daya Bay exhibit a mixture of species from tropical areas including South China Sea and Southeast Asia, and subtropical to temperate zones including East China Sea, Yellow Sea, Bohai Sea and sea areas around Japan (Li *et al*. 2008). The diversity of small to micro marine mollusk species collected by tangle nets from shallow water in Daya Bay result from the currents to some extent, which is influenced by the South China Sea Warm Current and the coastal current along Guangdong. The former flows year-round from southwest to northeast in the northern region of the South China Sea, and the later flows southward in winter and northward in summer. Although Daya Bay is a semi-enclosed bay where ocean currents generally flow at slower speeds due to topographic blocking, it is enough for empty micro shells from the subtidal zone to be carried by currents to shallow areas, especially by stronger waves triggered by typhoons. As a result, most specimens were collected as empty shells or shells with hermit crabs in the tangle nets sampling examined by the authors. However, there were still some small to medium-sized shells were collected alive, as currents also bring plankton to Daya Bay, which serve as nutrients for mollusks (Wang *et al.* 2004). The sandy-gravel seabed of

Daya Bay, composed of fragmented corals, also provides a habitat for mollusks. In addition to natural factors, Daya Bay hosts numerous shellfish farms. The artificially supplied feed for shell raising disperses into the seawater and nourish many shallow-water mollusk species.

Figure 1. Shells in tangle nets on the harbour of Daya Bay and mixed shells picked up from the tangle nets. Photos: Ji-Lin Jiang.

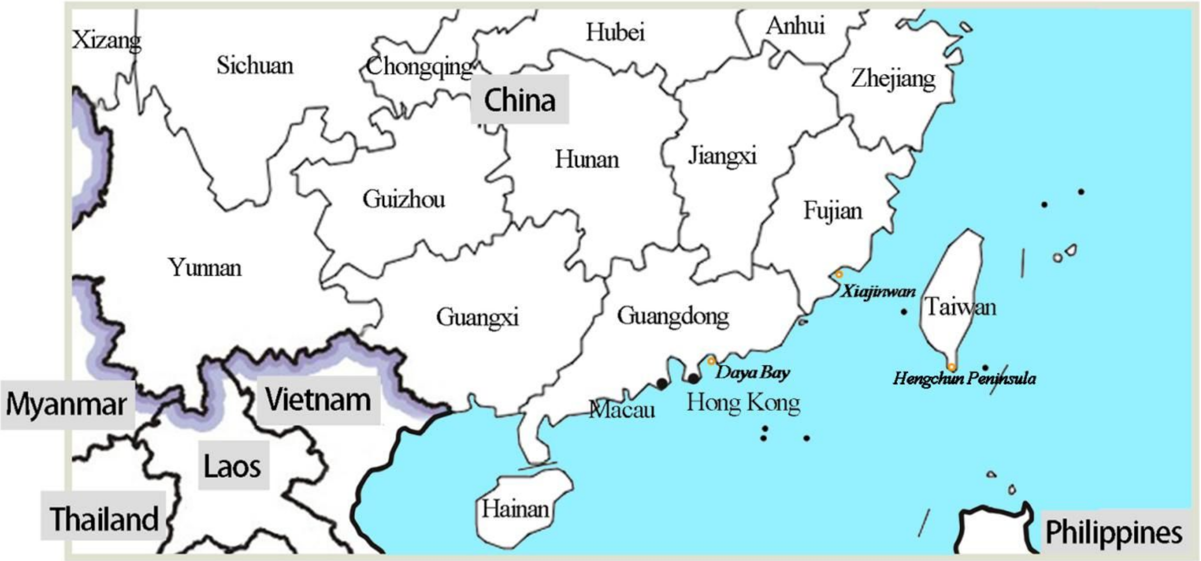
Xizang
Sichuan
Chongqing
China
Hubei
Anhui
Zhejiang
Hunan
Jiangxi
Guizhou
Fujian
Yunnan
Guangxi
Guangdong
Xiajinwan
Taiwan
Daya Bay
Hengchun Peninsula
Myanmar
Vietnam
Macau
Hong Kong
Laos
Thailand
Hainan
Philippines

Figure 2. A map of Daya Bay and its adjacent areas.

Systematics

Class Gastropoda Cuvier 1798
Family Tornidae Sacco, 1896 (1884)
Genus *Pseudoliotia* Tate, 1898
Type species: *Cyclostrema micans* A. Adams, 1850 = *Pseudoliotia micans* (A. Adams, 1850)

Pseudoliotia tankaorum n. sp. (Fig. 3. A–C)
https://zoobank.org/NomenclaturalActs/8aeb4b6a-3a2c-4314-959b-617f34e6c5be

Type locality. China, Guangdong Province, Huizhou City [惠州市], Daya Bay [大亚湾]; 22°43’N, 114°32’E; in shell grit collected by tangle nets from 5–10 m deep, leg. Ji-Lin Jiang.

Type material (8 shells). *Holotype:* CHINA • 1 shell (Fig. 3. A); Daya Bay; 22°43’N, 114°32’E; in shell grit collected by tangle nets from 5–10 m deep; Nov.-2024; SCSMBC240281. *Paratype 1*: CHINA • 1 shell; same data as holotype; SCSMBC240272. *Paratype 2*: CHINA • 1 shell (Fig. 3. B & C); juvenile, same data as holotype; SY. *Paratypes 3–5*: CHINA • 3 shells; same data as holotype; LLW. *Paratypes 6–7*: CHINA • 2 shells; same data as holotype; JJL.

Etymology. This name is dedicated to the Tanka People, also known as boat dwellers, who primarily live on junks or stilt houses along coastal regions for generations and compose several traditional aquatic communities in southern and eastern China.

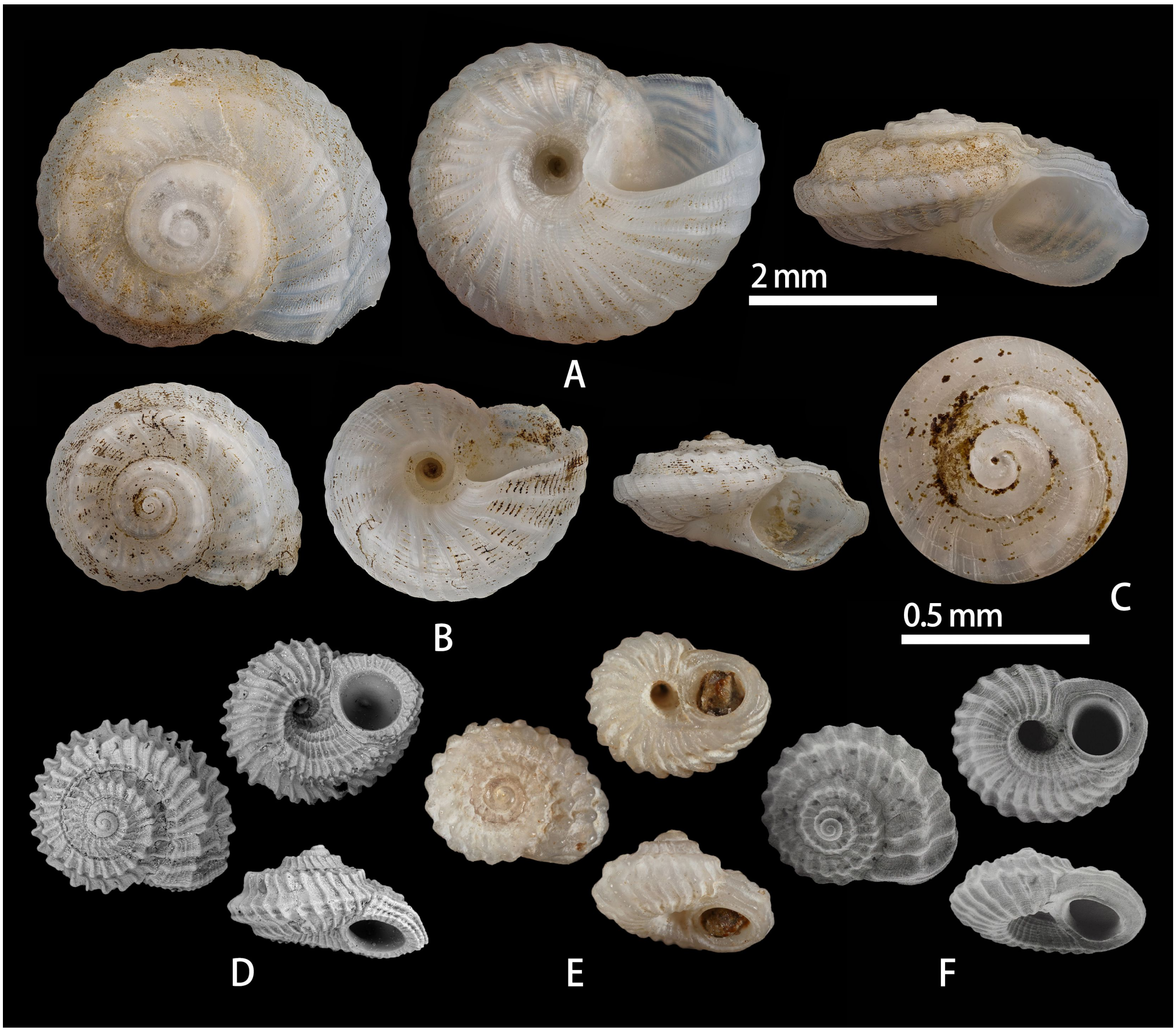

Figure 3. A-C. *Pseudoliotia* ***tankaorum*** n. sp. **A, C.** Holotype SCSMBC240281, 3.79×1.90 mm: C - detail of protoconch, **B.** Paratype 2 SY, 2.70×1.48 mm, **D.** *Pseudoliotia oscostata* Rubio & Rol á n, 2018, holotype MNHN-IM-2000-34128, 2.17×1.23 mm, © Mus é um national d'Histoire naturelle, Paris (France), **E.** *Pseudoliotia godeti* (Dautzenberg & Fischer, 1907), syntype MNHN-IM-2000-31163, 2×1.3 mm, © Mus é um national d'Histoire naturelle, Paris (France), **F.** *Pseudoliotia dispersa* Rubio & Rol á n, 2018, holotype MNHN-IM-2000-34125, 2.1×1.1 mm, photos in Rubio F. & Rol á n E. 2018. Photos: A-C by Shao Yang.

Description: Shell medium-siezd for this genus, white to cream, solid and robust, turbiniform, depressed, adult shell formed by 4 ½ whorls separated by a moderately deep suture, deeply and widely umbilicate.

Protoconch smooth, with 2 whorls, protruding from the rest of the shell. Teleoconch with approximately 2 ½ very convex whorls ornamented with thick carinae, spiral cordlets and axial ribs. Four thick carinae and around 30 axial ribs on the last whorl. The subsutural carina obtuse, less prominent, forming an angle of 95°–150° which increases gradually as shell grows. Two peripheral carinae prominent and almost flatly connected to form a thick spiral cord on the middle of the last whorl. The basal carina obtuse, rounded and indistinct. Space between the subsutural carina and the upper peripheral carina as well as space between the basal carina and the lower peripheral carina concave with angles of 120°–140° which also increases as shell grows. Thick nodules at the intersection of the axial folds with the carinae, which are prominent on the subsutural carina. Base convex with a basal carina and a periumbilical cord. Axial ribs arriving at the edge of the umbilicus and weakened inside the umbilicus. Thin spiral lines covering the teleoconch with around 68 lines on the last whorl between the suture and the basal carina.

Umbilicus broad and deep, inside with indistinct axial lines crossed by a spiral cord. Aperture slightly thickened for adult shells with a continuous peristome.

Aperture slightly elliptical, prosocline; parietal callus thick, continued into the columella which is thick and arched; outer lip with the crenulated margin formed by the termination of the spiral ribs.

Dimensions of the holotype: 1.90 mm in height and 3.79 mm in diameter.

Distribution: Only known from the type locality.

Differential diagnosis. The sculpture, carinae and umbilicus of this new species match the characters of "Micans Group" defined by Rubio & Rolán (2018), especially *Pseudoliotia oscostata* Rubio & Rolán, 2018 which also has two peripheral carinae almost flatly connected. However, this new species is larger than any other known species in this group, and its aperture is not thickened to form a round lip as *P. oscostata*, *Pseudoliotia godeti* (Dautzenberg & Fischer, 1907) and *Pseudoliotia dispersa* Rubio & Rolán, 2018.

Family Clathurellidae H. Adams & A. Adams, 1858
Genus *Etrema* Hedley, 1918
Type species: *Mangilia aliciae* Melvill & Standen, 1895 = *Etrema aliciae* (Melvill & Standen, 1895)

Etrema minyuensis n. sp. (Fig. 4. A-F, K-L)

https://zoobank.org/NomenclaturalActs/294af10e-6c50-4c19-8c67-ec032bdb57e3

Etrema alphonsianum (Hervier, 1896)– Lin & Rolán, 2024: 13, fig. 13. R.

Type locality. China, Guangdong Province, Huizhou City [惠州市], Daya Bay [大亚湾]; 22°43'N, 114°32'E; in shell grit collected by tangle nets from 5–10 m deep.
Type material (8 shells). *Holotype:* CHINA • 1 shell (Fig. 3. A–B); Daya Bay; 22°43'N, 114°32'E; in shell grit collected by tangle nets from 5–10 m deep; Nov.-2024; SCSMBC240273. *Paratype 1*: CHINA • 1 shell; same data as holotype; SCSMBC240274. *Paratype 2*: CHINA • 1 shell (Fig. 3. A–B); same data as holotype; SY. *Paratypes 3–5*: CHINA • 3 shells; same data as holotype; LLW. *Paratypes 6–7*: CHINA • 2 shells; same data as holotype; JJL.
Etymology. In administrative divisions of China, Fujian Province and Guangdong Province are respectively abbreviated as Min and Yue. This new species was firstly recorded from Xiamen, Fujian, and its type locality is in Huizhou, Guangdong.

Description: Shell of medium size for this genus, ovate-lanceolate with sharp apex and rounded, flaring outer lip, aperture sinuous. Teleoconches of 5½–6 whorls, rounded, spire elevate, pale yellow with dark brown subsutural region, margin of outer lip, the whole inner lip and its adjacent area on the last whorl. Varix and the protrusions formed by crossing ribs white, the concave part of strong spiral ridges brown. Last whorl constricted toward siphon to form a distinct waist. Suture shallow, subsutural region flattened. Siphonal canal wide, protruded, termination truncate and smooth. Anal sinus deep, linguiform, slightly constricted by the parietal pad. One shallow notch on the outer lip below the anal sinus. Aperture somewhat flabellate and elongate, approximately accounting for 32–37% of the shell length. Inner lip smooth, one moderately developed callus pad on parietal region and 2–5 weak plicae on the columella covered by dark brown inductura. Outer lip thickened with wide varix, inner edge white with 2 denticles, outer edge sinuous with around 7 protrusions formed by the spiral ribs on the last whorl.

Sculpture developed, cancellate with blunt axial ribs and narrower spiral ridges. Axial ribs weakly arcuate to straight, weakend near the suture, evenly spaced and the width approximately equal to the width of adjacent gaps of ribs. 11 axial ribs on each whorl. Spiral ribs thin and rounded to form ridges. 2 prominent ridges on teleoconch whorls, 1–2 indistinct spiral ribs above the first ridge. One relatively strong spiral rib below the second ridge covered partly or almost thoroughly by the suture and becoming the third strongest ridge on the last whorl. 15–16 strong or weak spiral ribs on the last whorl. Surface of the whole teleoconch covered with tiny nodules.

Protoconch white, conical with around 3¼ convex whorls. The first whorl tilted and smooth while one strong carina on the middle of remainder whorls.

Dimensions of the holotype: 6.72 mm in height and 2.46 mm in width.

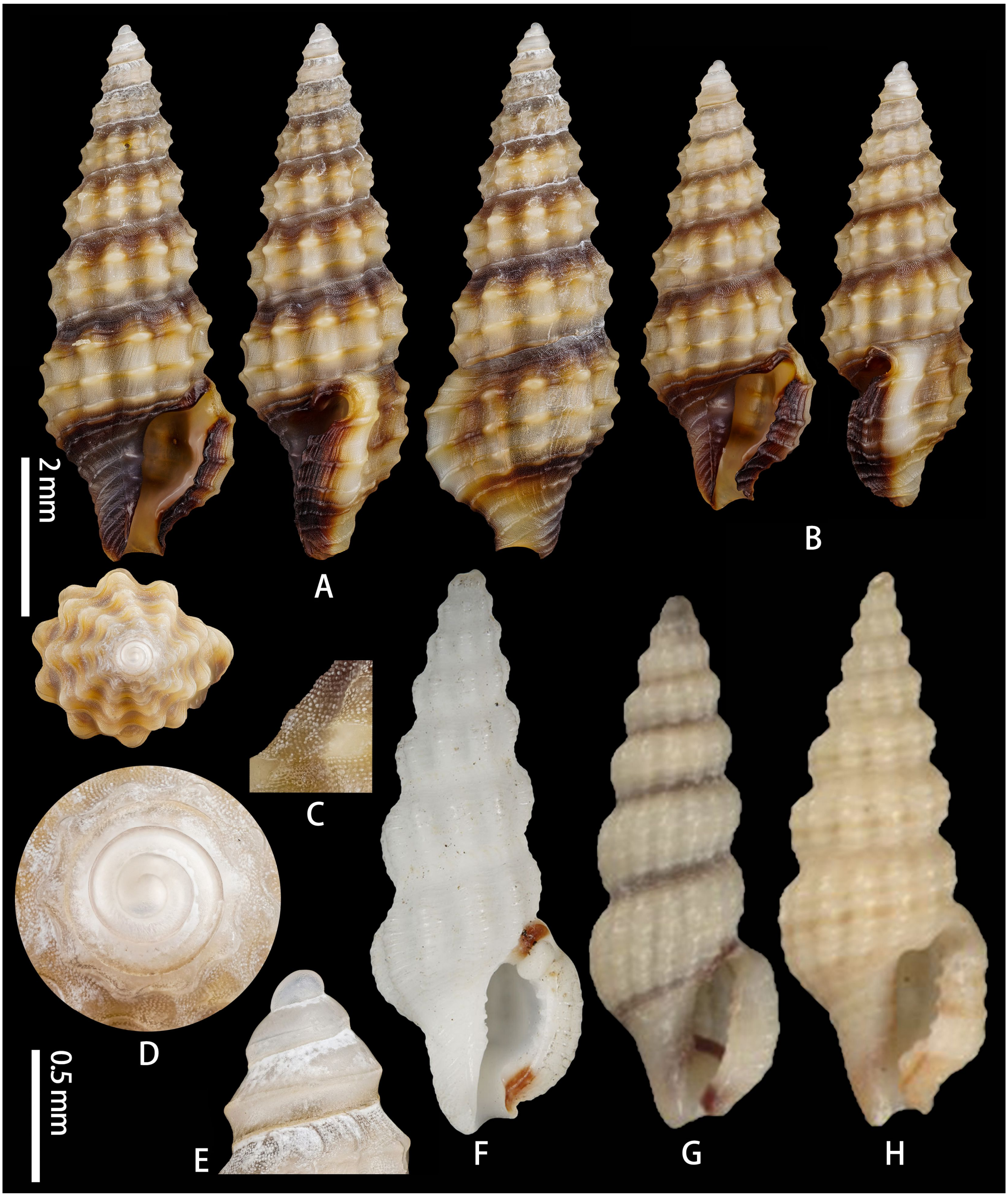

Figure 4. A–E. *Etrema* ***minyuensis*** n. sp. **A, C–E.** Holotype SCSMBC240273, 2.46×6.72 mm: C - detail of tiny nodules, D, E - details of protoconch, **B.** Paratype 2 SY, 2.18×5.61 mm, **F.** *Etrema aliciae* (Melvill & Standen, 1895), syntype (possible) MANCH.EE.3703, 3.6×9 mm, not to scale, © Manchester Museum, The University of Manchester., **G.** *Etrema scalarina* (Deshayes, 1863), syntype MNHN-IM-2000-2833, 3.1×8.4 mm, not to scale, © Muséum national d'Histoire naturelle, Paris (France), **H.** *Etrema alphonsiana* (Hervier, 1896), syntype MNHN-IM-2000-2730, 3.5×9.2 mm, not to scale, © Muséum national d'Histoire naturelle, Paris (France). Photos: A-E by Shao Yang.

Distribution: Known from the type locality and Xiajinwan, Xiamen, China.

Differential diagnosis. The two prominent spiral ridges of *Etrema minyuensis* n. sp. make it distinguished from all other *Etrema* species from China, Japan, Philippines or other neighbouring sea areas. Many *Etrema* species with light color have brown to black patterns on the aperture or subsutural region, such as

Etrema scalarina (Deshayes, 1863), *Etrema alphonsiana* (Hervier, 1896), *Etrema aliciae* (Melvill & Standen, 1895), *Etrema texta* (Dunker, 1860), *Etrema subauriformis* (Smith, 1879), etc. However, non of these species has such large areas of brown streaks and stainings which also appear intermittently on spiral ridges. *Etrema trigonostoma* (Hervier, 1896) from Loyalty Islands and *Etrema carinata* Bozzetti, L., 2009 from Madagascar have similar bi-carinae sculptures on the whorls, but the former has a stronger rib above the first prominent ridge, a light brown coloration throughout the shell and a shorter siphon, and the later has a rather weak first prominent ridge and sparser axial ribs on the whorls. Some species of *Nannodiella* Dall, 1919, such as *Nannodiella acricula* (Hedley, 1922), also have similar carinal protoconch and two prominent spiral ridges on teleoconches, but *Nannodiella* species have shorter spires different from most *Etrema*, and the proportion of the protoconch's size to the total length is greater for *Nannodiella*.

Family Mangeliidae Fischer, 1883
Genus *Guraleus* Hedley, 1918
Type species: *Mangelia picta* A. Adams & Angas, 1864 = *Guraleus pictus* (A. Adams & Angas, 1864)

Guraleus yangzhiganlu n. sp. (Fig. 5. A-F)

https://zoobank.org/NomenclaturalActs/cc046db0-5cb9-415f-b857-ccc4901804c3

Type locality. China, Guangdong Province, Huizhou City [惠州市], Daya Bay [大亚湾]; 22°43’N, 114°32’E; in shell grit collected by tangle nets from 5–10 m deep.
Type material (8 shells). *Holotype:* CHINA • 1 shell (Fig. 3. A–B); Daya Bay; 22°43’N, 114°32’E; in shell grit collected by tangle nets from 5–10 m deep; Nov.-2024; SCSMBC240275. *Paratype 1*: CHINA • 1 shell; same data as holotype; SCSMBC240276. *Paratype 2*: CHINA • 1 shell (Fig. 3. A–B); same data as holotype; SY. *Paratypes 3–5*: CHINA • 3 shells; same data as holotype; LLW. *Paratypes 6–7*: CHINA • 2 shells; same data as holotype; JJL.
Etymology. Yangzhi Ganlu is a Chinese dessert originated from Hong Kong made from mango, sago, pomelo and coconut milk, which indicates the coloration of this new species.

Description: Shell of medium size for this genus, semi-fusiform with sharp apex and rounded, flaring outer lip, aperture sinuous. Teleoconches of 4½–5 whorls, rounded, spire elevate, apricot yellow, spiral ribs light yellow, varix of aperture white and margin of outer lip dark brown. Last whorl constricted toward siphon to form a waist. Suture slightly impressed. Siphonal canal short and wide, constricted, termination slightly obliquely truncate and smooth. Anal sinus open and deep, spout-like, at about 120° to shell axis, shallowly linguiform, lying on the strongest spiral rib. Aperture ovate, elongate, approximately accounting for 30–40% of the shell length. Inner lip smooth, parietal region concave with moderately developed callus, slightly recurved or straight before siphonal canal. One slight protrusion on the parietal region near the anal sinus. Outer lip thickened with wide varix, inner edge with 2–3 denticles, the one near anal sinus protruded and the others elongated and weak. corresponded with the termination of spiral ribs on the last whorl.

Sculpture developed, cancellate with strong axial ribs crossed by thinner spiral ribs. 19–21 spiral ribs on the last whorl and 4 on the other whorls of teleoconch interspersed with very fine spiral cords. The 2 spiral ribs below the suture weak and the other 2 spiral ribs below these 2 ribs prominent. Around 10 wide and thickened axial ribs on each whorl which extend from suture to suture and align from whorl to whorl. Raised small nodules formed by intersection of axial ribs and spiral ribs.

Protoconch conical with around 3½ convex whorls. The first two whorls smooth while around 20 gradually increasing axial ribs on the rest of protoconch.

Dimensions of the holotype: 5.90 mm in height and 2.39 mm in width.

Distribution: Only known from the type locality.

Differential diagnosis. Guraleus yangzhiganlu n. sp. has a unique coloration in the genus *Guraleus* Hedley, 1918. Moreover, its shape and sculpture differ from other species from western Pacific. *Guraleus kamakuranus* (Pilsbry, 1904) and *Guraleus himerodes* (Melvill & Standen, 1896) have more angulate whorls and the spiral ribs are weaker. *Guraleus semicarinata* (Pilsbry, 1904) and *Guraleus deshayesii* (Dunker, 1860) have denser axial ribs and slenderer outlines.

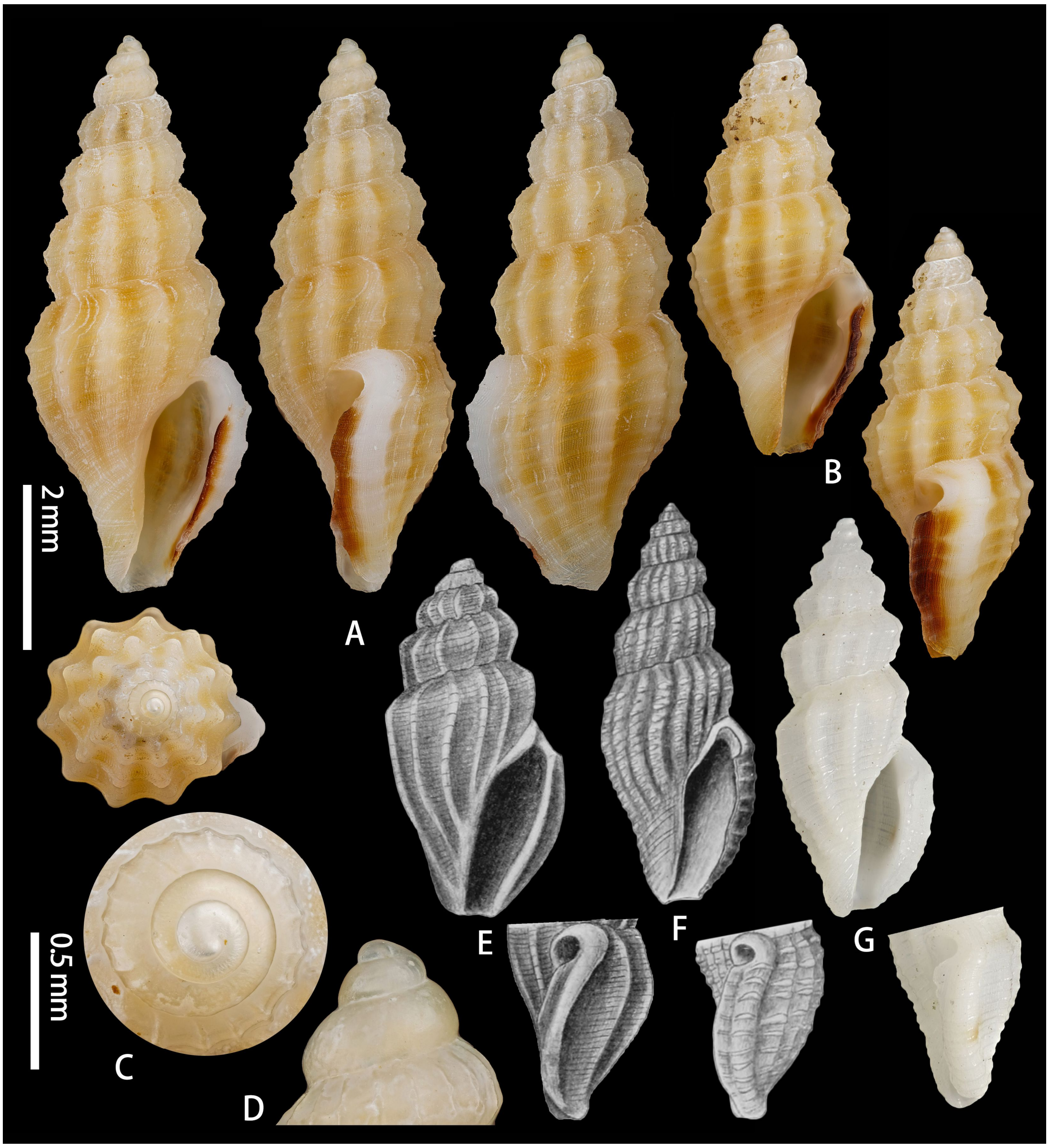

Figure 5. A-D. *Guraleus* ***yangzhiganlu*** n. sp. **A, C, D.** Holotype SCSMBC240275, 2.39×5.90 mm: C, D - details of protoconch, **B.** Paratype 2 SY, 2.00×4.61 mm, **E.** *Guraleus kamakuranus* (Pilsbry, 1904) in original description, 2.3×4.7 mm, not to scale, **F.** *Guraleus semicarinata* (Pilsbry, 1904) in original description, 2.7×7 mm, not to scale, **G.** *Guraleus himerodes* (Melvill & Standen, 1896), syntype MANCH.EE.3744, 2.64×6.50 mm, © Manchester Museum, The University of Manchester. Photos: A-D by Shao Yang.

Family Horaiclavidae Bouchet, Kantor, Sysoev & Puillandre, 2011
Genus *Graciliclava* Shuto, 1983
Type species: *Graciliclava mackayensis* Shuto, 1983 = *Graciliclava costata* (Hedley, 1922)

Graciliclava fulvocincta (G. Nevill & H. Nevill, 1875) n. comb. (Fig. 5. A-F)

Mangelia fulvocincta G. Nevill & H. Nevill, 1875: 85, pl. 7 fig. 1.
Pseudorhaphitoma hervieri (Hedley, 1922)– Lin & Rolán, 2024: 13, fig. 13. Y.

Type locality. Bombay.
Type material. According to G. Nevill & H. Nevill, 1875, the type materials were deposited in Indian Museum and the collection of H. Nevill. Not examined by the authors.
Material examined. Daya Bay, China; 22°43’N, 114°32’E; in shell grit collected by tangle nets from 5–10 m deep, leg. Ji-Lin Jiang; Nov.-2024; SCSMBC240277. Xiajinwan, China; 24°31’N, 118°12’E; in sand sediment near the high-water line, leg. Li-Wen Lin; Apr.-Nov.-2022; SCSMBC240278.

Remarks: No more records of this mysterious species have been seen after its original description. This species is characterised by the peculiar and strong carina on the third and the fourth whorls, the other five longitudinally and varicosely ribbed whorls, dense spiral lines, the chestnut-brown bands under the suture and the obsolate anal sinus. G. Nevill & H. Nevill, 1875 described and figured this species precisely, which made it possible to identify the specimens from Daya Bay according to these materials. Considering the changes in taxonomy after its description, its generic status becomes questionable. Neatly arranged axial ribs and very shallow anal sinus match the character of some genera of Mangeliidae (*e.g. Pseudorhaphitoma* O. Boettger, 1895 and *Citharomangelia* Kilburn, 1992) and Horaiclavidae (*e.g. Anacithara* Hedley, 1922 *and Horaiclavus* Oyama, 1954). However, the protoconch of this species is closer to many genera of Clathurellidae (*e.g. Etrema* Hedley, 1918, *Nannodiella* Dall, 1919 and *Etremopsis* Powell, 1942) by containing 3¾–4 whorls, which are smooth for the first whorl and strongly carinate for remainder ones. All these features indicate this species belongs to *Graciliclava* Shuto, 1983, whose type species *Graciliclava mackayensis* Shuto, 1983 was described from northeastern Australia. This genus was placed firstly in Mangeliidae and then transferred to Horaiclavidae through morphology by Bouchet *et al.* (2011).

Distribution: Bombay, Ceylon and Pooree in the original description; Daya Bay and Xiajinwan, China.

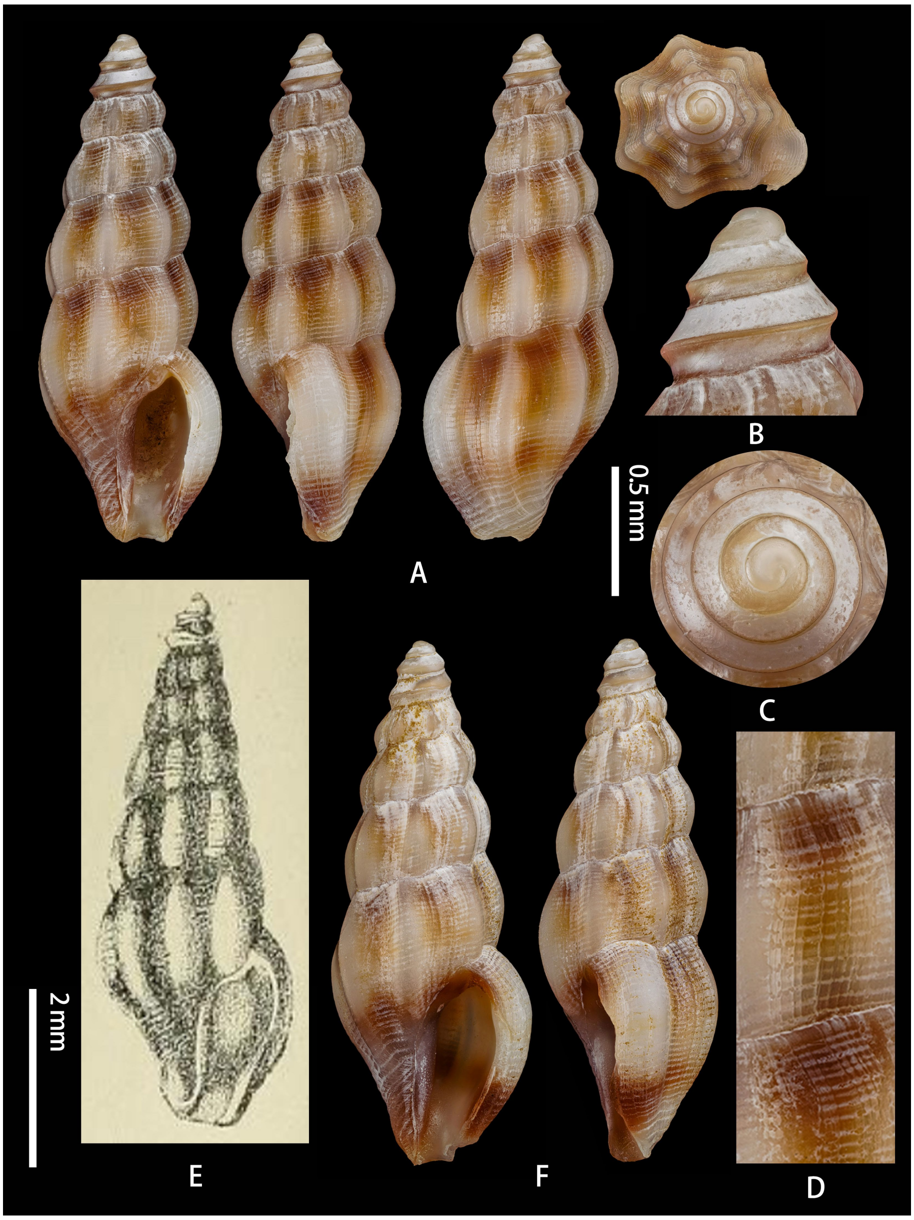

Figure 6. *Graciliclava fulvocincta* (G. Nevill & H. Nevill, 1875). **A-D.** SCSMBC240277, 2.12×5.84 mm: details of the specimen (B-D), **E.** *G. fulvocincta* in original description (G. Nevill & H. Nevill, 1875), 8 mm in height, not to scale, **F.** SY, 2.29×6.01 mm. Photos: A-D & F by Shao Yang.

Family Raphitomidae Bellardi, 1875

Genus *Kermia* W. R. B. Oliver, 1915
Type species: *Kermia benhami* W. R. B. Oliver, 1915

Kermia feitian n. sp. (Fig. 5. A-F)

Zoobank registration:
https://zoobank.org/NomenclaturalActs/2f2e252d-eab3-4a9c-82e5-e5027b3aa133

Kuroshiodaphne saturata (Reeve, 1845)– Lin & Rolán, 2024: 13, fig. 6. J–K & fig. 11. L.

Type locality. China, Guangdong Province, Huizhou City [惠州市], Daya Bay [大亚湾]; 22°43'N, 114°32'E; in shell grit collected by tangle nets from 5–10 m deep.
Type material (8 shells). *Holotype:* CHINA • 1 shell (Fig. 7. A, C, D); Daya Bay; 22°43'N, 114°32'E; in shell grit collected by tangle nets from 5–10 m deep; Nov.-2024; SCSMBC240279. *Paratype 1*: CHINA • 1 shell; same data as holotype; SCSMBC240280. *Paratype 2*: CHINA • 1 shell (Fig. 7. B); same data as holotype; SY. *Paratypes 3–5*: CHINA • 3 shells; same data as holotype; LLW. *Paratypes 6–7*: CHINA • 2 shells; same data as holotype; JJL.
Etymology. Feitian, or "Flying Apsaras", are iconic motifs in Chinese Buddhist art which are widely used for wall paintings and statuaries. The oblique brown stripes on the shells are reminiscent of the Feitian patterns.

Description: Shell of large size for this genus, semi-fusiform with sharp apex and rounded, flaring outer lip, aperture sinuous. Teleoconches of 5½–6 whorls, rounded, spire elevate, white to light brown with oblique dark brown stripes, narrow brown ribbon below the suture and one wide brown ribbon on the middle of the last whorl, large brown plaque near the aperture. Last whorl constricted toward siphon to form a shallow waist. Suture slightly impressed. Siphonal canal short and wide, constricted, termination slightly obliquely truncate and smooth. Anal sinus open U-shaped, spout-like, at about 125° to shell axis, shallowly linguiform, opening constricted, directed anteriorly. Aperture ovate, elongate, approximately accounting for 40% of the shell length. Inner lip smooth, parietal region concave with moderately developed callus, recurved before siphonal canal. Outer lip thickened with wide and shallow varix, inner edge with 9–10 blunt small denticles corresponded with the termination of spiral ribs on the last whorl.

Sculpture developed, cancellate with and strong spiral ribs crossed by indistinct axial ribs which devide spiral ribs into segments. 18–20 spiral ribs on the last whorl and 7 spiral ribs on the other whorls of teleoconch. The 2 spiral ribs below the suture weaker and very close together to make the shoulder almost absent.

Protoconch conical with 4–4¼ slightly convex whorls, cancellate sculpture on the surface which becomes diagonal in the last two whorls, translucently white, thin and fragile and always intact or missing for adult shells.

Dimensions of the holotype: 8.39 mm in height and 2.86 mm in diameter.

Distribution: Known from the type locality and Xiajinwan, Xiamen, China.

Differential diagnosis. Kermia feitian n. sp. is a large species for *Kermia* Oliver, 1915. *Kermia daedalea* (Garrett, 1873), *Kermia producta* (Pease, 1860) and *Kermia felina* (Reeve, 1843) are species with similar size and elongate fusiform shape. *K. daedalea* and *K. producta* have a rather wide distribution from central-western Pacific to South Africa. Both two species differ by having larger protoconch with deep coloration, narrower anal sinus, more distinct shoulder and deeper waist. *K. felina* is closest with this new species in shape and outline, but its sculpture is more prominent to form small nodules, and its color spots are almost randomly distributed. *Kermia benhami* Oliver, 1915 has similar shape and sculpture but the spiral ribs are sparser, the waist is deeper and it is only half the size of this new species.

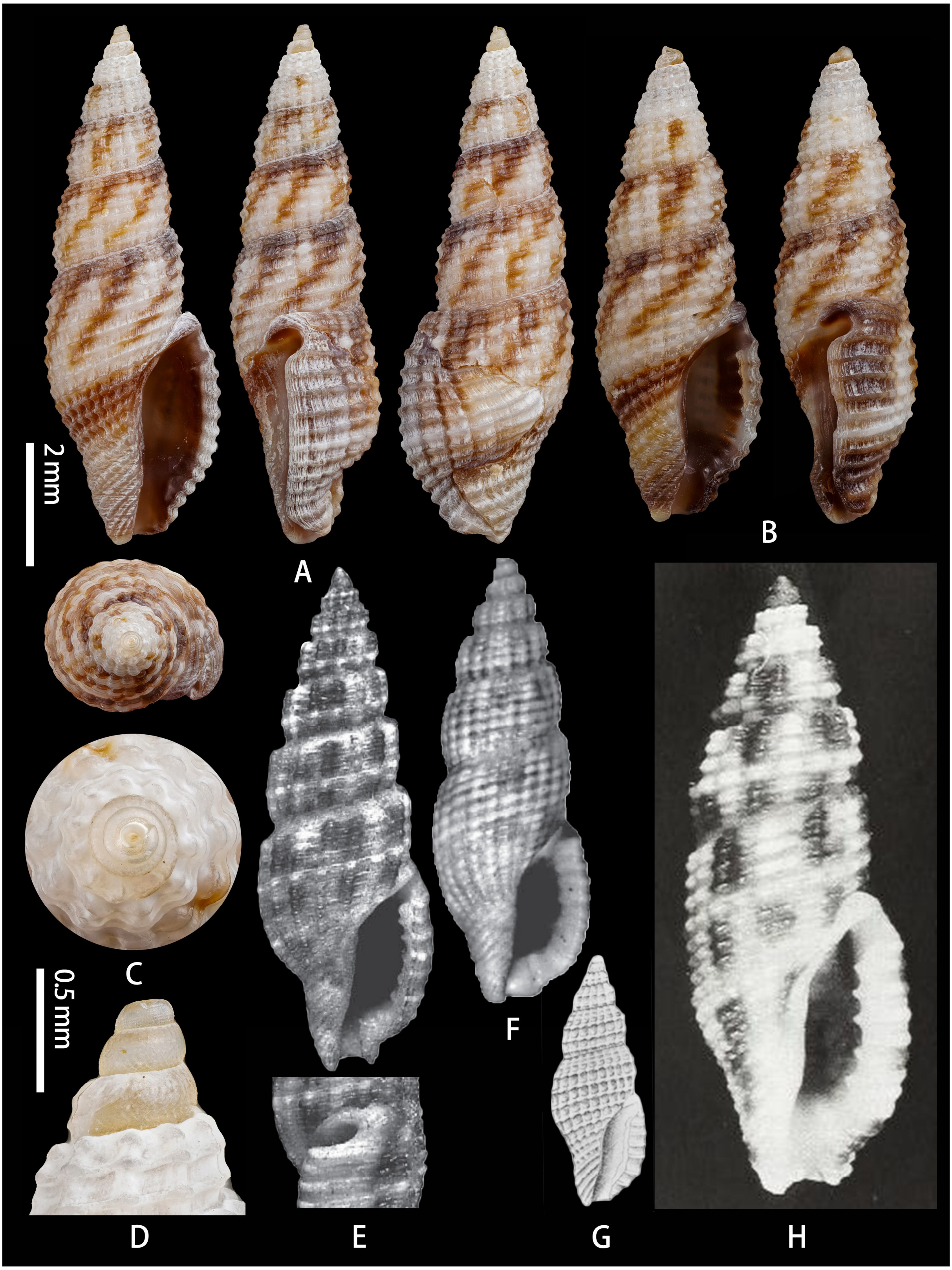

Figure 7. A-D. *Kermia* ***feitian*** n. sp. **A, C, D.** Holotype SCSMBC240279, 2.86×8.39 mm: C, D - details of protoconch, **D.** Paratype 2 SY, 2.70×7.71 mm, **E.** *Kermia daedalea* (Garrett, 1873), lectotype ANSP 15821, 2.7×8.1 mm, photos in Kilburn R. N. 2009. **F.** *Kermia producta* (Pease, 1860), lectotype BMNH 1962761, 2.6×7.2 mm, photo in Kilburn R. N. 2009. **G.** *Kermia benhami* W. R. B. Oliver, 1915 in original description, 1.5×4 mm, **H.** *Kermia felina* (Reeve, 1843), SD, 3.7×10 mm, photo in Shasky D.R. 1997. Photos: A-D by Shao Yang.

Checklist of species recorded in shell grit collected by tangle nets from Daya Bay

*The criteria of the abundance of individuals of each species in sediments: + for less than 5, ++ for 5~10, +++ for 10~25, ++++ for 25~50 and +++++ for more than 50 per 3000 pieces.
Species marked with ★ also appear in sand sediment from Xiajinwan, Xiamen, China.

Family	Species	Abundance*	Figure
Chilodontaidae	*Vaceuchelus clathratus* (A. Adams, 1853) ★	++	Fig. 14. A
Chilodontaidae	*Euchelus scaber* (Linnaeus, 1758) ★	+++	Fig. 9. P
Fissurellidae	*Diodora mus* (Reeve, 1850) ★	+++	Fig. 13. F
Trochidae	*Conotalopia musiva* (Gould, 1861) ★	++++	Fig. 14. C
Trochidae	*Pseudominolia sulcifera* (A. Adams, 1855)	++	Fig. 13. J
Trochidae	*Clanculus* sp.	+	Fig. 13. A
Calliostomatidae	*Calliostoma spesa* J.-L. Zhang, Wei & S.-P. Zhang, 2018	+	Fig. 12. L
Skeneidae	*Leucorhynchia* sp.	++	Fig. 15. B
Conradiidae	*Conradia doliaris* A. Adams, 1863	++	Fig. 16. K
Phasianellidae	*Tricolia aethiopica* (Philippi, 1853)	++	Fig. 15. L
Cerithiidae	*Clypeomorus* cf. *pellucida* (Hombron & Jacquinot, 1848)	+	Fig. 9. E
Planaxidae	*Fossarus multicostatus* Pease, 1861	++++	Fig. 16. H
Dialidae	*Diala semistriata* (Philippi, 1849) ★	+	Fig. 16. A
Turritellidae	*Turritella cingulifera* Sowerby I, 1825	++++	Fig. 9. L
Epitoniidae	*Amaea foulisi* Kilburn, 1985	+++	Fig. 10. C
Epitoniidae	*Opalia* cf. *mormulaeformis* (Masahito, Kuroda & Habe, 1971)	++	Fig. 11. A
Epitoniidae	*Epitonium coretum* (Iredale, 1936) ★	++	Fig. 9. Q
Epitoniidae	*Epitonium* sp.	+	Fig. 16. I
Epitoniidae	*Epidendrium* sp.	+	Fig. 15. F
Epitoniidae	*Epitonium castum* (Sowerby II, 1873)	++	Fig. 12. I–J
Epitoniidae	*Gyroscala xenicima* (Melvill & Standen, 1903)	+	Fig. 10. I
Epitoniidae	*Epitonium* cf. *townsendi* (Melvill & Standen, 1903)	+	Fig. 14. K
Littorinidae	*Echinolittorina radiata* (Souleyet in Eydoux & Souleyet, 1852)	+++	Fig. 15. G
Littorinidae	*Echinolittorina malaccana* (Philippi, 1847)	+++	Fig. 11. H
Naticidae	*Notocochlis* cf. *cernica* (Jousseaume, 1874)	++	Fig. 14. H
Naticidae	*Mammilla* sp.	+	Fig. 12. K
Triphoridae	*Viriola tricincta* (Dunker, 1882) ★	+++	Fig. 10. K
Triphoridae	*Bouchetriphora confusa* (Kosuge, 1963)	++	Fig. 11. B
Rissoinidae	*Phosinella dunkerina* Kuroda & Habe, 1961	++	Fig. 14. D
Rissoinidae	*Rissoina ambigua* (Gould, 1849)	++	Fig. 12. D
Rissoinidae	*Rissoina sculptilis* Garrett, 1873	++	Fig. 13. H
Zebinidae	*Stosicia annulata* (Dunker, 1860) ★	+++	Fig. 15. C
Vitrinellidae	*Circulus cinguliferus* (A. Adams, 1850) ★	++++	Fig. 16. D
Vitrinellidae	*Pseudoliotia tankaorum* n. sp.	++	Fig. 15. D
Vitrinellidae	*Vitrinella* sp.	+	Fig. 15. E
Tornidae	*Anticlimax obesa* Rubio & Rolán, 2014 ★	+	Fig. 16. B
Eulimidae	*Melanella* sp.	+	Fig. 14. E
Eulimidae	*Vitreolina* sp.	+	Fig. 11. K
Eulimidae	*Melanella yamazii* (Habe, 1952)	+	Fig. 15. K
Iravadiidae	*Pseudonoba yendoi* (Yokoyama, 1927) ★	+	Fig. 13. G
Vanikoridae	*Vanikoro hairoinsularis* Lin & Rolán, 2024 ★	+++	Fig. 16. E
Vanikoridae	*Japanonoba patula* (A. Adams, 1863)	++	Fig. 16. G
Vanikoridae	*Macromphalus jinyuae* Lin, 2023 ★	++++	Fig. 14. F
Vanikoridae	*Macromphalus yamamotoi* (Habe, 1978)	++	Fig. 15. H

Family	Species	Abundance*	Figure
Vanikoridae	*Macromphalus tornatilis* (Gould, 1859) ★	++	Fig. 16. L
Vanikoridae	*Berthais egregia* (A. Adams, 1863)	+++++	Fig. 15. A
Vanikoridae	*Vanikoro fenestrata* (A. Adams, 1863)	++++	Fig. 11. L–M
Calyptraeidae	*Desmaulus extinctorium* (Lamarck, 1822)	+	Fig. 10. G
Ovulidae	*Phenacovolva barbieri* Lorenz & Fehse, 2009	+	Fig. 9. M
Cancellariidae	*Trigonostoma thysthlon* Petit & Harasewych, 1987 ★	+	Fig. 9. C
Columbellidae	*Mitrella bicincta* (Gould, 1860)	++	Fig. 10. L
Columbellidae	*Indomitrella puella* (Sowerby II, 1844)	+++	Fig. 10. H
Columbellidae	*Mitrella pudica* (Brazier, 1877) ★	+++	Fig. 13. I
Columbellidae	*Zafra pumila* (Dunker, 1858) ★	+++	Fig. 16. C
Nassariidae	*Nassarius* cf. *crebricostatus* (Schepman, 1911)	++	Fig. 9. F
Nassariidae	*Nassarius smithii* (Marrat, 1877) ★	+	Fig. 9. O
Nassariidae	*Nassarius succinctus* (A. Adams, 1852)	++	Fig. 9. K
Nassariidae	*Nassarius* aff. *tabescens* (Marrat, 1880)	+	Fig. 14. G
Nassariidae	*Reticunassa paupera* (Gould, 1850) ★	+++	Fig. 9. I
Pisaniidae	*Engina concinna* (Reeve, 1846) ★	++	Fig. 9. D
Muricidae	*Bedevina birileffi* (Lischke, 1871) ★	++++	Fig. 9. J
Muricidae	*Indothais* sp.	+++	Fig. 9. N
Olividae	*Olivella* cf. *mandarina* (Duclos, 1835)	++	Fig. 12. F
Ancillariidae	*Amalda* sp.	+	Fig. 10. Q
Clathurellidae	*Etrema minyuensis* n. sp. ★	+++++	Fig. 11. G
Clathurellidae	*Paraclathurella contracta* (Reeve, 1843) ★	+++	Fig. 13. B
Raphitomidae	*Pseudodaphnella leuckarti* (Dunker, 1860)	+	Fig. 13. C
Clathurellidae	*Pseudoetrema fortilirata* (Smith, 1879)	+++	Fig. 12. B
Borsoniidae	*Tomopleura coffea* (Thiele, 1925)	++	Fig. 9. A
Drilliidae	*Splendrillia* sp.	+	Fig. 10. B
Horaiclavidae	*Epideira multiseriata* (Smith, 1877)	+	Fig. 9. B
Horaiclavidae	*Paradrillia sultana* (Thiele, 1925)	+++	Fig. 10. J
Horaiclavidae	*Anacithara* cf. *ione* (Melvill & Standen, 1896) ★	++	Fig. 12. A
Mangeliidae	*Pseudorhaphitoma fulvocincta* (G. Nevill & H. Nevill, 1875) ★	++++	Fig. 12. H
Mangeliidae	*Guraleus* sp.	+	Fig. 12. C
Mangeliidae	*Cytharopsis radulina* Kuroda & Oyama, 1971	+	Fig. 10. A
Mangeliidae	*Guraleus semicarinatus* (Pilsbry, 1904) ★	+++	Fig. 10. P
Mangeliidae	*Guraleus yangzhiganlu* n. sp. ★	++++	Fig. 14. I
Mangeliidae	*Guraleus kamakuranus* (Pilsbry, 1904)	+	Fig. 14. J
Mangeliidae	*Hemicythara octangulata* (Dunker, 1860)	+	Fig. 13. E
Raphitomidae	*Kermia feitian* n.sp.	++++	Fig. 10. N
Raphitomidae	*Kermia pumila* (Mighels, 1845) ★	++	Fig. 13. D
Raphitomidae	*Pseudodaphnella* cf. *tincta* (Reeve, 1846) ★	+++	Fig. 15. I
Raphitomidae	*Veprecula pungens* (Gould, 1860) ★	++	Fig. 10. O
Raphitomidae	*Pleurotomella* sp.	+	Fig. 11. J
Terebridae	*Granuliterebra bathyrhaphe* (Smith, 1875)	++	Fig. 10. D
Architectonicidae	*Heliacus* cf. *cerdaleus* (Melvill & Standen, 1903)	+++	Fig. 14. B
Mathildidae	*Mathilda* cf. *sinensis* Fischer, 1867	++	Fig. 11. I
Acteonidae	*Pupa sekii* Habe, 1958	+++++	Fig. 12. E
Cylichnidae	*Cylichna sibogae* Schepman, 1913 ★	++++	Fig. 11. F
Retusidae	*Pyrunculus phialus* (A. Adams, 1862)	++	Fig. 15. J
Ringiculidae	*Ringicula doliaris* Gould, 1860	++++	Fig. 16. J
Amathinidae	*Monotygma digitalis* (Dall & Bartsch, 1906) ★	+	Fig. 12. G
Pyramidellidae	*Styloptygma* sp.	+	Fig. 10. M
Pyramidellidae	*Turbonilla pseudomultigyrata* Nomura, 1936	++	Fig. 11. C
Pyramidellidae	*Turbonilla terebra* A. Adams, 1861	++	Fig. 11. E
Pyramidellidae	*Turbonilla* cf. *loiclegoffi* Peñas & Rolán, 2010 ★	++	Fig. 11. D

Family	Species	Abundance*	Figure
Pyramidellidae	*Menestho* sp.	+	Fig. 16. F
Pyramidellidae	*Megastomia tenera* (A. Adams, 1860) ★	+++	Fig. 14. L
Plicatulidae	*Plicatula regularis* Philippi, 1849 ★	+++	Fig. 10. F
Dentaliidae	*Dentalium octangulatum* Donovan, 1804	+++	Fig. 9. G
Gadilidae	*Gadila virginalis* (Boissevain, 1906) ★	+++	Fig. 10. E
Laevidentaliidae	*Laevidentalium* sp.	+++	Fig. 9. H

CONCLUSIONS

The diversity of mollusk species in the shell grit collected by tangle nets reflects the mollusk species living in the intertidal zones of Dayawan, Huizhou and species from adjacent subtidal zones or deeper areas, especially the dominant species. The taxonomic studies of mollusks from this area enriches the knowledge of marine mollusk from southern China. However, almost all micro shell specimens collected by tangle nets from this area were empty or with hermit crabs. Sampling methods is expected to be improved, such as using the Filipino lumun-lumun nets which will help to collect living individuals and make researches of soft parts of by anatomical and molecular methods feasible.

CORRECTIONS AND UPDATES

Some corrections are made here on Lin & Rolán, 2024. *Minolia strigata* Sowerby III, 1894 is now synonymized with *Conotalopia musiva* (Gould, 1861) and placed in Trochidae (see Huang, 2025). *Graciliclava fulvocincta* (G. Nevill & H. Nevill, 1875), *Pseudoetrema fortilirata* (Smith, 1879), *Pseudodaphnella* cf. *tincta* (Reeve, 1846) and *Pyrgulina* cf. *shigeyasui* (Yokoyama, 1927) was respectively misidentified as *Pseudorhaphitoma hervieri* (Hedley, 1922), *Pseudorhaphitoma fuscescens* (Thiele, 1925), *Pseudodaphnella barnardi* (Brazier, 1876) and *Narvaliscala percancellata* (Nakayama, 2000). *Murchisonella* cf. *densistriata* (Nomura, 1936) was an *Ebala* species and described as *Ebala yuzan* Lin & Shao, 2024 later. Severely eroded shells misidentified as *Etrema alphonsianum* (Hervier, 1896) and *Kuroshiodaphne saturata* (Reeve, 1845) are described as *Etrema minyuensis* n. sp. and *Kermia feitian* n. sp. in this paper. The sculpture and outline of *Mathilda amanda* Thiele, 1925 in Lin & Rolán, 2024 matches the original description and figures of *Mathilda sinensis* Fischer, 1867, while the *Mathilda* pieces from Daya Bay have denser and weaker axial ribs.

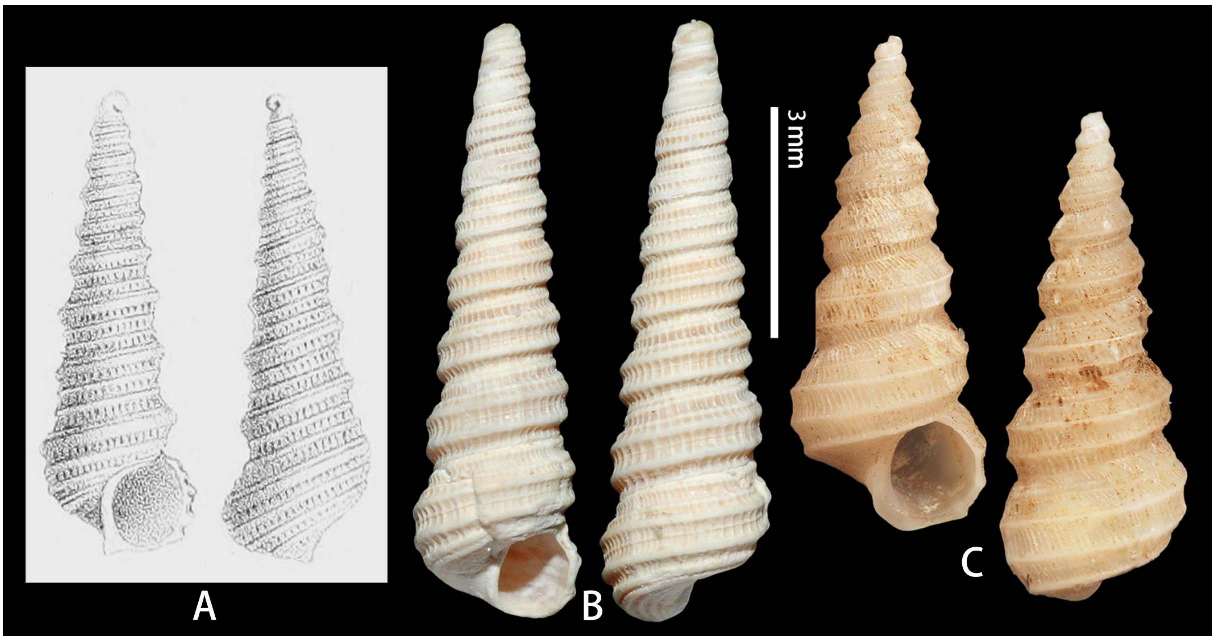

Figure 8. A. *Mathilda sinensis* P. Fischer, 1867 in original description. **B.** *Mathilda sinensis* from Xiajinwan, Xiamen. **C.** *Mathilda* cf. *sinensis* from Daya Bay, Huizhou.

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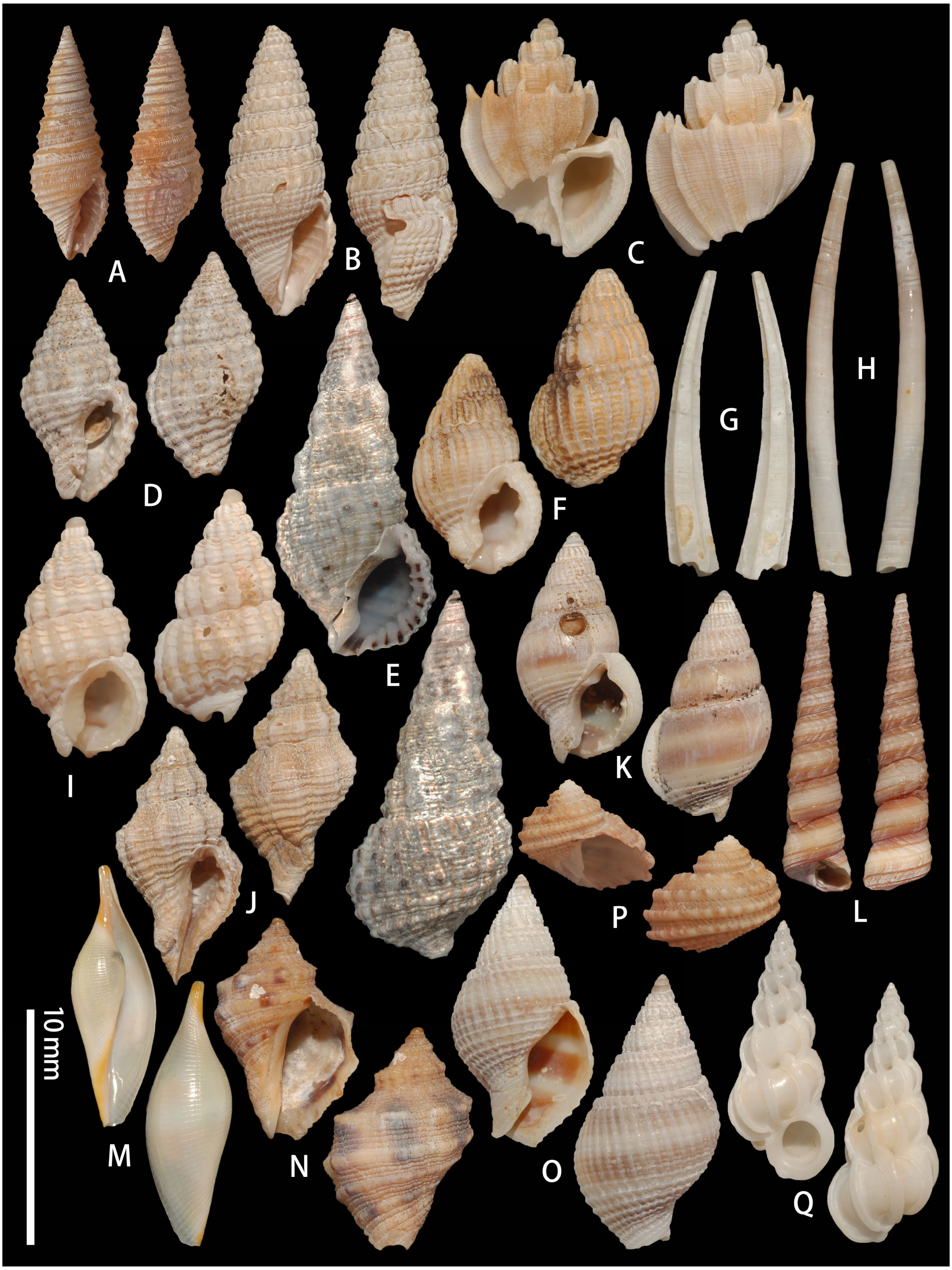

Figure 9. Specimens from Daya Bay. A: *Tomopleura coffea* (Thiele, 1925); B: *Epideira multiseriata* (Smith, 1877); C: *Trigonostoma thysthlon* Petit & Harasewych, 1987; D: *Engina concinna* (Reeve, 1846); E: *Clypeomorus* cf. *pellucida* (Hombron & Jacquinot, 1848); F: *Nassarius* cf. *crebricostatus* (Schepman, 1911); G: *Dentalium octangulatum* Donovan, 1804, juvenile; H: *Laevidentalium sp.*; I : *Reticunassa paupera* (Gould, 1850); J: *Bedevina birileffi* (Lischke, 1871); K: *Nassarius succinctus* (A. Adams, 1852); L: *Turritella cingulifera* Sowerby I, 1825; M: *Phenacovolva barbieri* Lorenz & Fehse, 2009, juvenile; N: *Indothais* sp., juvenile; O: *Nassarius smithii* (Marrat, 1877), juvenile; P: *Euchelus scaber* (Linnaeus, 1758); Q: *Epitonium coretum* (Iredale, 1936). Photos: Li-Wen Lin.

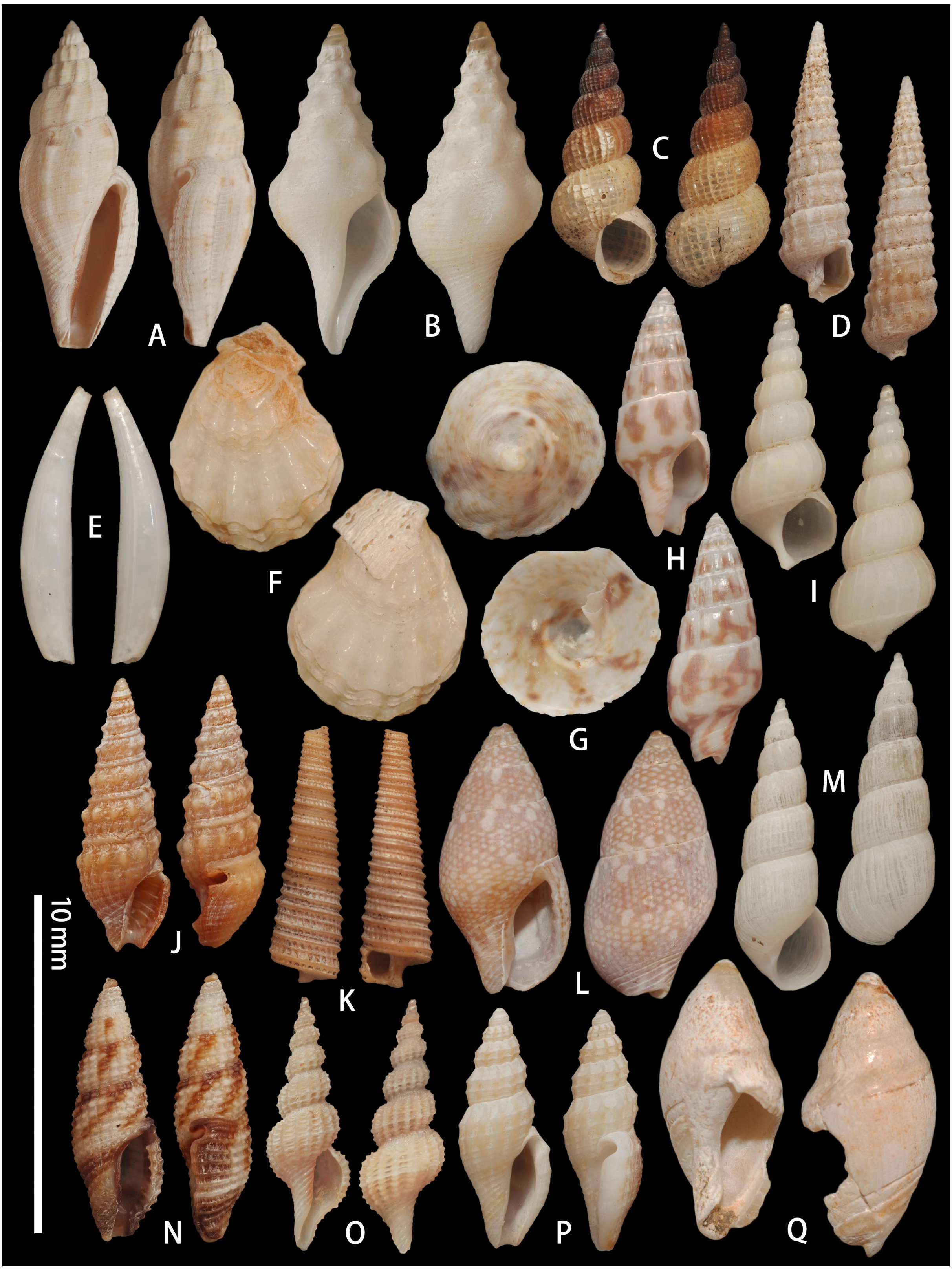

Figure 10. Specimens from Daya Bay. A: *Cytharopsis radulina* Kuroda & Oyama, 1971; B: *Splendrillia* sp., juvenile; C: *Amaea foulisi* Kilburn, 1985; D: *Granuliterebra bathyrhaphe* (Smith, 1875); E: *Gadila virginalis* (Boissevain, 1906); F: *Plicatula regularis* Philippi, 1849; G: *Desmaulus extinctorium* (Lamarck, 1822); H: *Indomitrella puella* (Sowerby II, 1844); I: *Gyroscala xenicima* (Melvill & Standen, 1903); J: *Paradrillia sultana* (Thiele, 1925)*;* K: *Viriola tricincta* (Dunker, 1882); L: *Mitrella bicincta* (Gould, 1860); M: *Styloptygma* sp.; N: *Kermia feitian* n. sp.; O: *Veprecula pungens* (Gould, 1860); P: *Guraleus semicarinatus* (Pilsbry, 1904); Q: *Amalda* sp., juvenile. Photos: Li-Wen Lin.

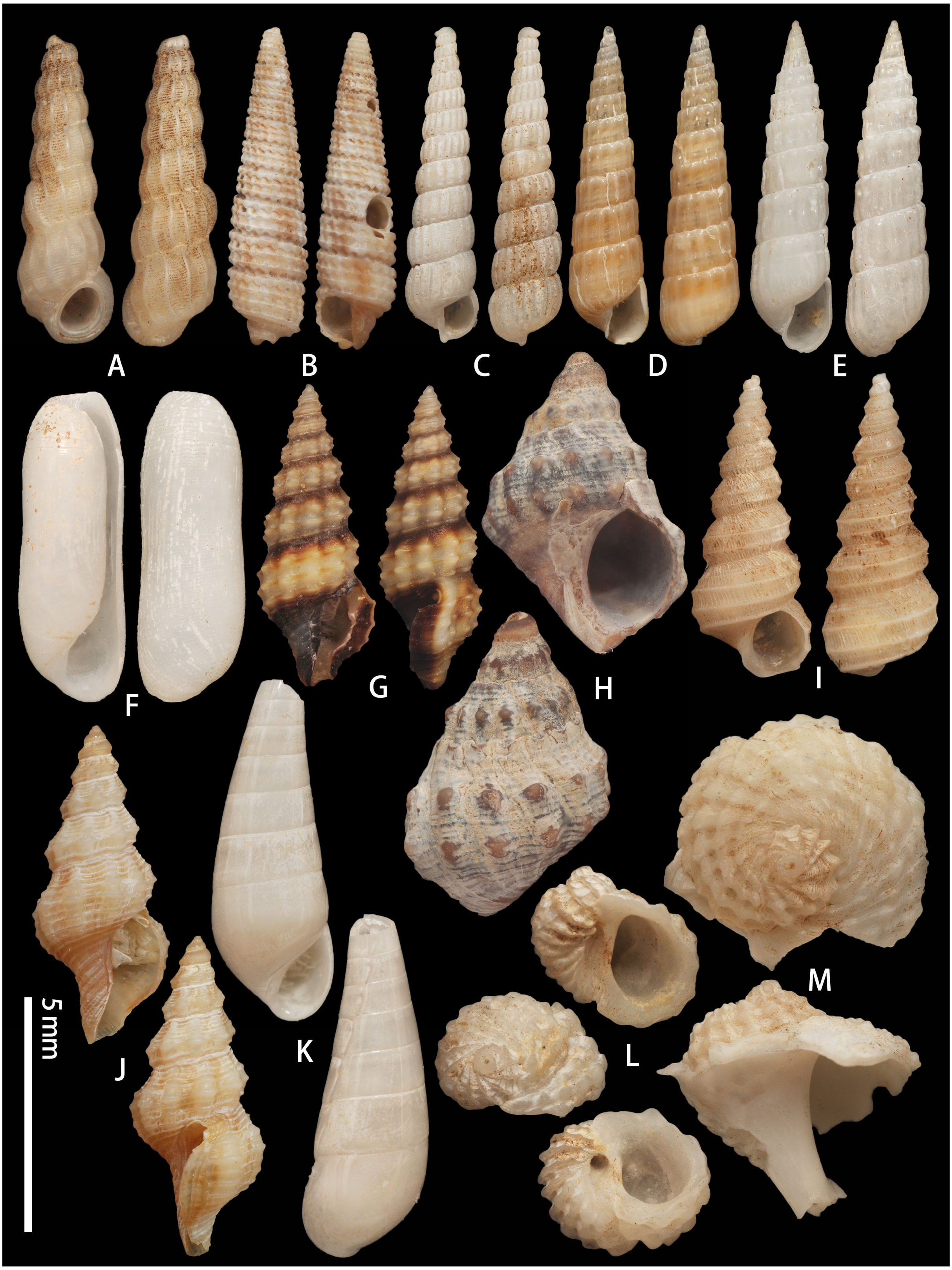

Figure 11. Specimens from Daya Bay. A: *Opalia* cf. *mormulaeformis* (Masahito, Kuroda & Habe, 1971); B: *Bouchetriphora confusa* (Kosuge, 1963); C: *Turbonilla pseudomultigyrata* Nomura, 1936; D: *Turbonilla* cf. *loiclegoffi* Peñas & Rolán, 2010; E: *Turbonilla terebra* A. Adams, 1861; F: *Cylichna sibogae* Schepman, 1913; G: *Etrema minyuensis* n. sp.; H: *Echinolittorina malaccana* (Philippi, 1847); I: *Mathilda* cf. *sinensis* Fischer, 1867; J: *Pleurotomella* sp.; K: *Vitreolina* sp.; L–M: *Vanikoro fenestrata* (A. Adams, 1863), juvenile. *Photos: Li-Wen Lin.*

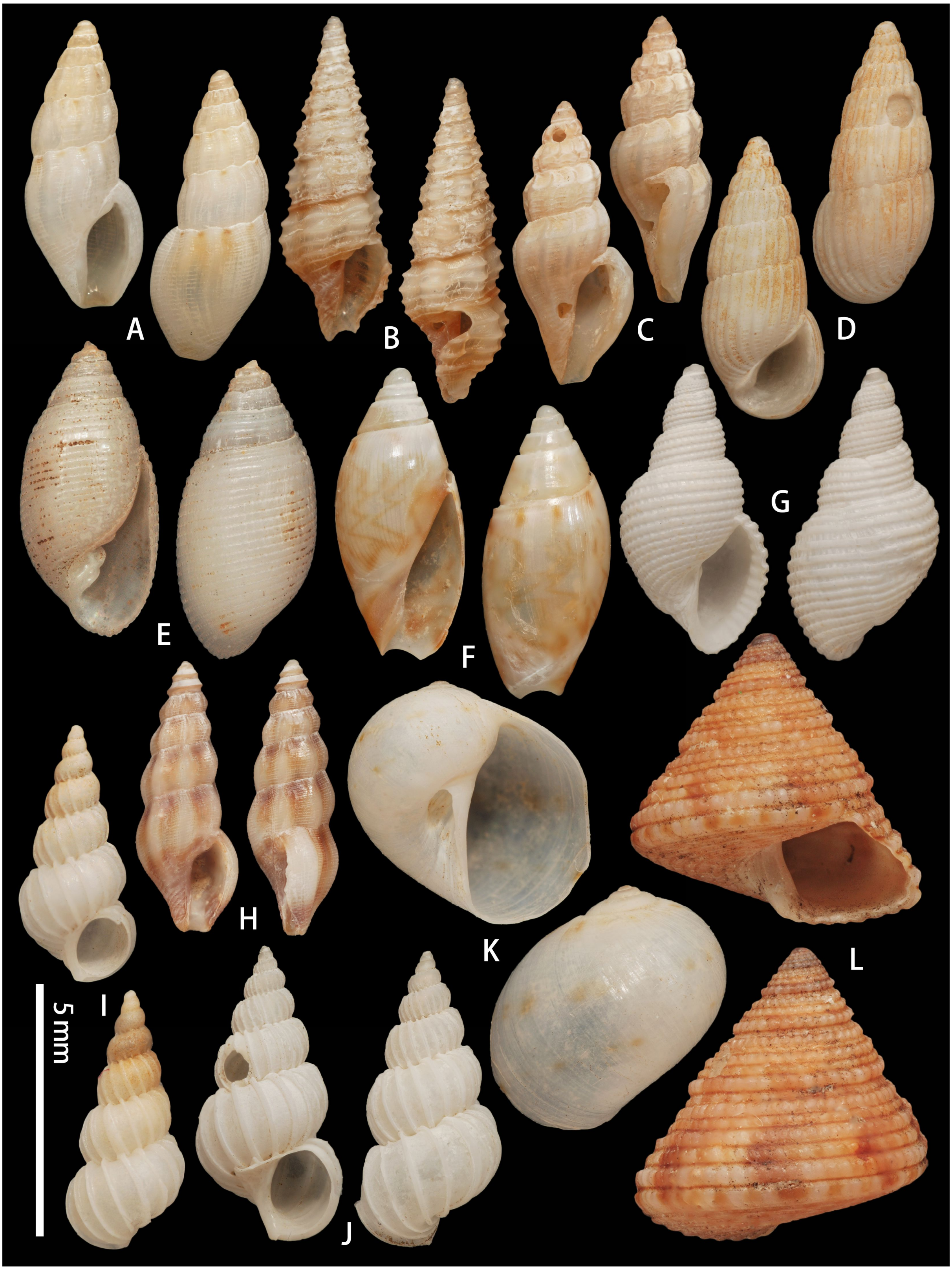

Figure 12. Specimens from Daya Bay. A: *Anacithara* cf. *ione* (Melvill & Standen, 1896); B: *Pseudoetrema fortilirata* (Smith, 1879); C: *Guraleus* sp.; D: *Rissoina ambigua* (A. Gould, 1849); E: *Pupa sekii* Habe, 1958; F: *Olivella* cf. *mandarina* (Duclos, 1835); G: *Monotygma digitalis* (Dall & Bartsch, 1906); H: *Pseudorhaphitoma fulvocincta* (G. Nevill & H. Nevill, 1875); I–J: *Epitonium castum* (Sowerby II, 1873); K: *Mammilla* sp., juvenile; L: *Calliostoma spesa* J.-L. Zhang, Wei & S.-P. Zhang, 2018. Photos: Li-Wen Lin.

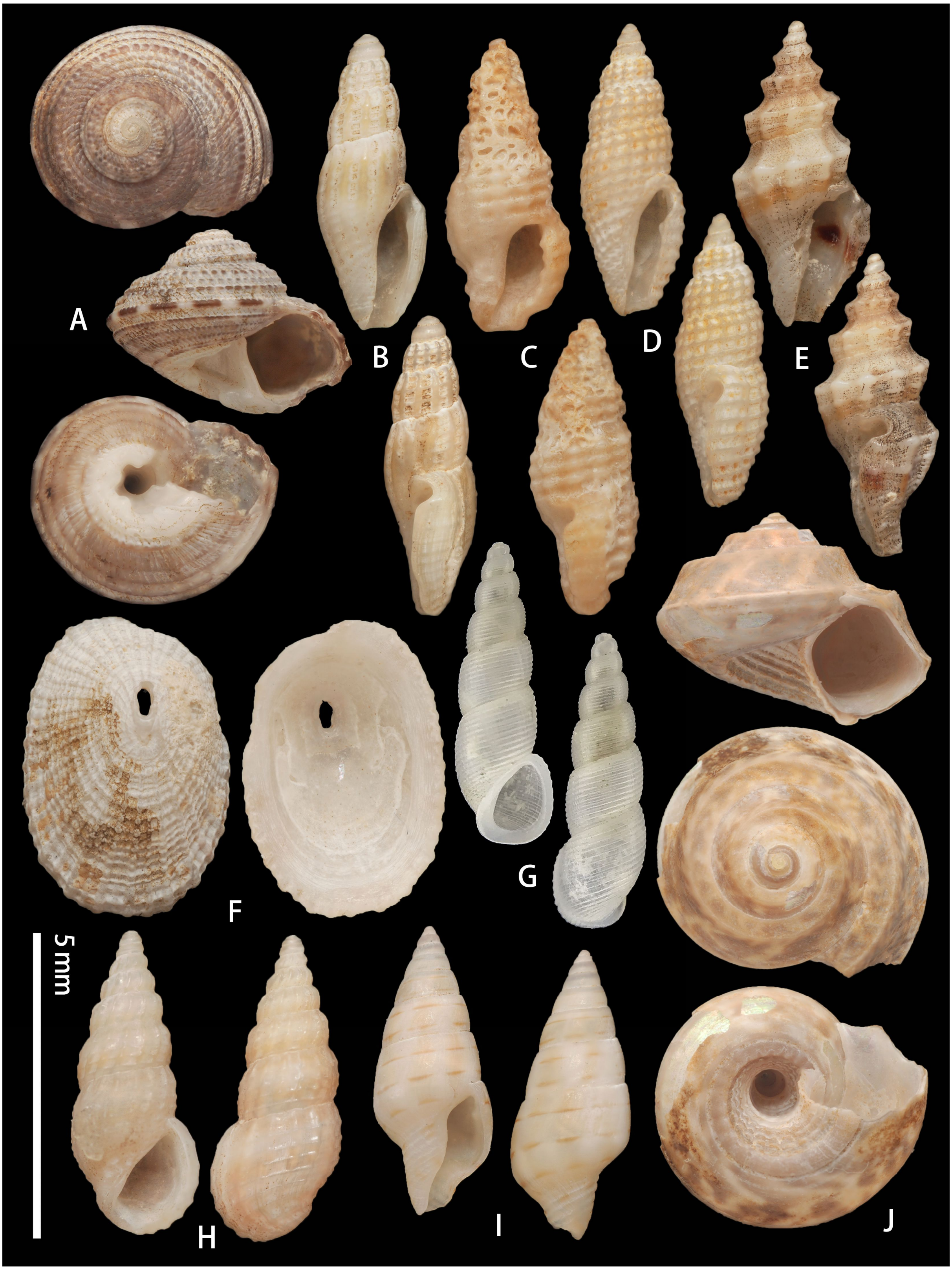

Figure 13. Specimens from Daya Bay. A: *Clanculus* sp., juvenile; B: *Paraclathurella contracta* (Reeve, 1843); C: *Pseudodaphnella leuckarti* (Dunker, 1860); D: *Kermia pumila* (Mighels, 1845); E: *Hemicythara octangulata* (Dunker, 1860); F: *Diodora mus* (Reeve, 1850); G: *Pseudonoba yendoi* (Yokoyama, 1927); H: *Rissoina sculptilis* Garrett, 1873; I: *Mitrella pudica* (Brazier, 1877); J: *Pseudominolia sulcifera* (A. Adams, 1855). Photos: G by Ji-Lin Jiang, others by Li-Wen Lin.

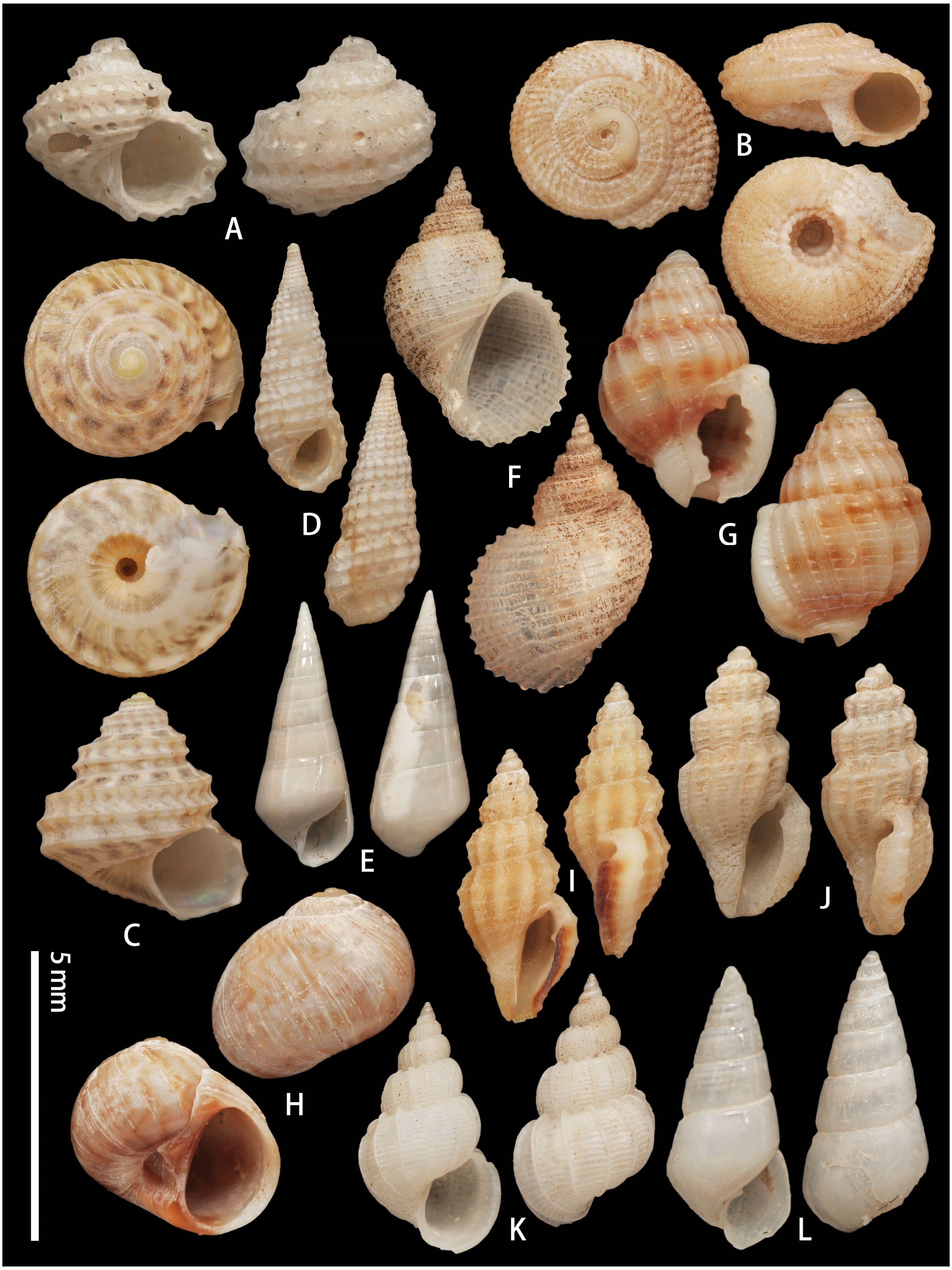

Figure 14. Specimens from Daya Bay. A: *Vaceuchelus clathratus* (A.Adams, 1853); B: *Heliacus* cf. *cerdaleus* (Melvill & Standen, 1903); C: *Conotalopia musiva* (Gould, 1861); D: *Phosinella dunkerina* Kuroda & Habe, 1961; E: *Melanella* sp.; F: *Macromphalus jinyuae* Lin, 2023; G: *Nassarius* aff. *tabescens* (Marrat, 1880); H: *Notocochlis* cf. *cernica* (Jousseaume, 1874), juvenile; I: *Guraleus yangzhiganlu* n. sp.; J: *Guraleus kamakuranus* (Pilsbry, 1904); K: *Epitonium* cf. *townsendi* (Melvill & Standen, 1903); L: *Megastomia tenera* (A. Adams, 1860). Photos: Li-Wen Lin.

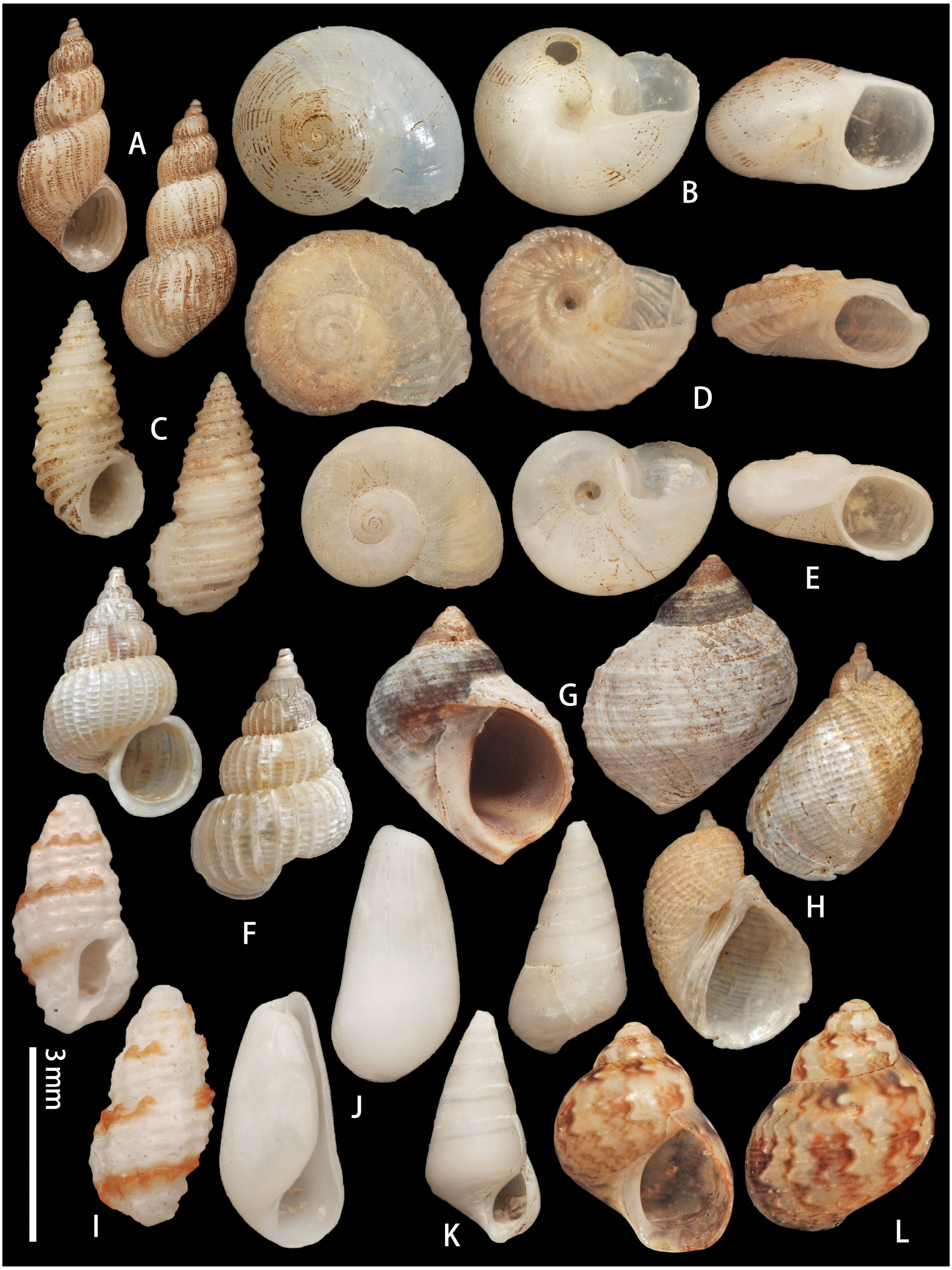

Figure 15. Specimens from Daya Bay. A: *Berthais egregia* (A. Adams, 1863); B: *Leucorhynchia* sp.; C: *Stosicia annulata* (Dunker, 1860); D: *Pseudoliotia tankaorum* n. sp.; E: *Vitrinella* sp.; F: *Epidendrium* sp.; G: *Echinolittorina radiata* (Souleyet in Eydoux & Souleyet, 1852); H: *Macromphalus yamamotoi* (Habe, 1978); I: *Pseudodaphnella* cf. *tincta* (Reeve, 1846); J: *Pyrunculus phialus* (A. Adams, 1862); K: *Melanella yamazii* (Habe, 1952); L: *Tricolia aethiopica* (Philippi, 1853). Photos: Li-Wen Lin.

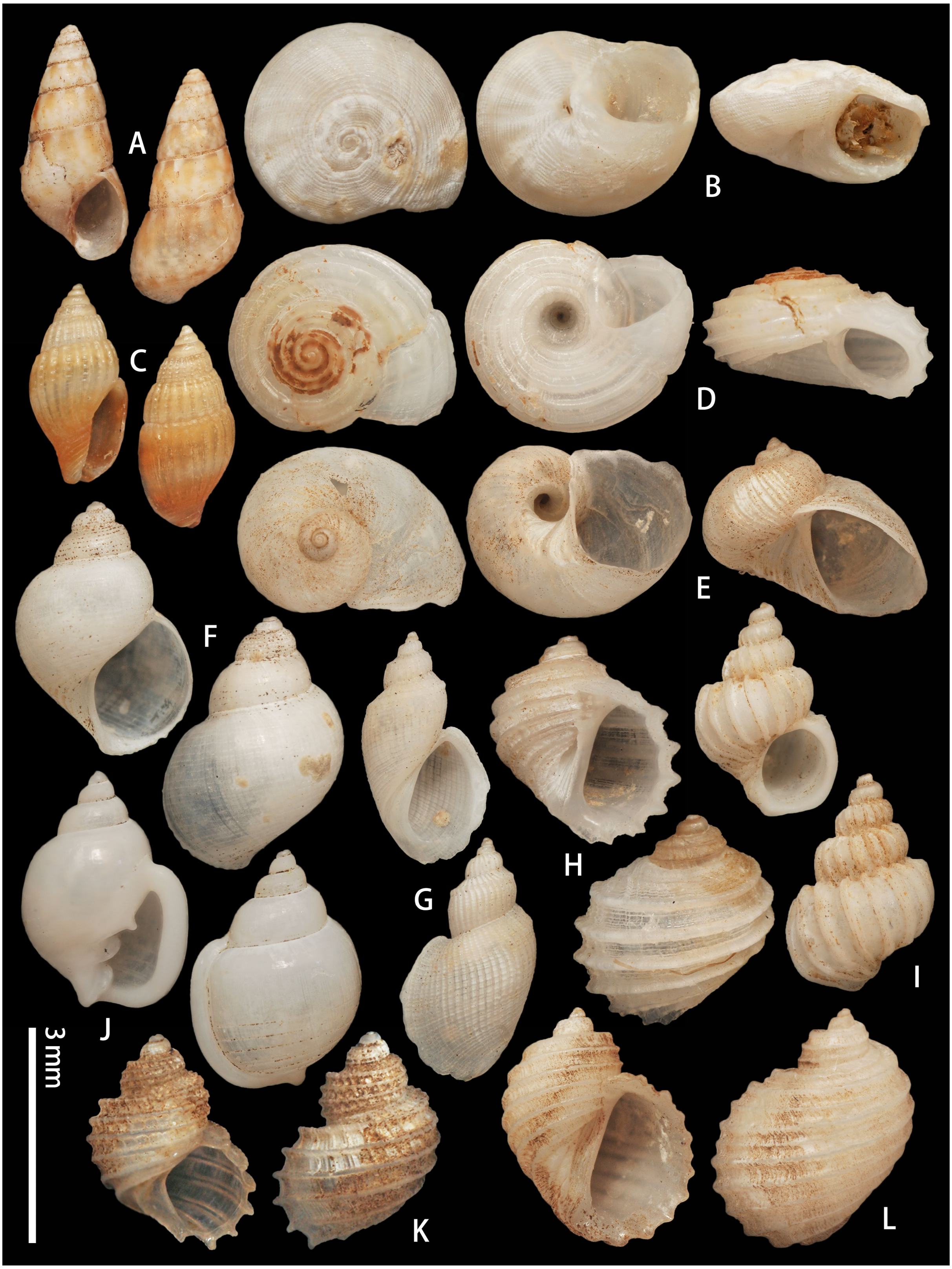

Figure 16. Specimens from Daya Bay. A: *Diala semistriata* (Philippi, 1849); B: *Anticlimax obesa* Rubio & Rolán, 2014, juvenile*;* C: *Zafra pumila* (Dunker, 1858); D: *Circulus cinguliferus* (A. Adams, 1850); E: *Vanikoro hairoinsularis* Lin & Rol ά n, 2024; F: *Menestho* sp.; G: *Japanonoba patula* (A. Adams, 1863); H: *Fossarus multicostatus* Pease, 1861; I: *Epitonium* sp.; J: *Ringicula doliaris* Gould, 1860; K: *Conradia doliaris* A. Adams, 1863; L: *Macromphalus tornatilis* (Gould, 1859). Photos: Li-Wen Lin.

Première occurrence de l'Anomiidae motile *Enigmonia* Iredale, 1918 (Bivalvia, Pectinida) dans le Bartonien (Éocène moyen) du bassin d'Aquitaine et description d'une espèce nouvelle

Jean-Michel PACAUD [1], Sébastien COPPINI [2], Sébastien BUISSON [3] & Frédéric MEUNIER [4]

[1] CR2P Centre de Recherche en Paléontologie – Paris,
Muséum national d'Histoire naturelle, Sorbonne Université, CNRS,
57 rue Cuvier, CP 38, 75005 Paris (France)
E-mail : pacaud@mnhn.fr

[2] 30 rue Lantiez, 75017 paris
E-mail : bigfish027@hotmail.com

[3] 11 rue Adélaide Hautval, Résidence Vauban, Appt A103, 33390 Blaye
E-mail : sebbuisson5@gmail.com

[4] 18 rue Denis Papin, 33400 Talence
E-mail : meunier.frederic@gmail.com

https://zoobank.org/References/8EB731EA-F515-4557-AEDC-3BC8F7CC333E

Résumé. L'espèce nouvelle *Enigmonia silossa* nov. sp., provenant des argiles sableuses bartoniennes (Éocène moyen) de Horsarrieu [Pédelail] (Landes), est décrite et figurée. Cette découverte est importante à plus d'un titre. En premier lieu, c'est la première occurrence fossile de l'Anomiidae motile *Enigmonia* Iredale, 1918 dans le bassin d'Aquitaine. C'est également le premier signalement de ce genre dans des sédiments du Bartonien (Éocène moyen) et singulièrement, c'est le premier exemplaire aux valves en connexion récolté dans le registre fossile montrant ainsi une valve droite, jusqu'ici inconnue. La présence et la conservation parfaite de nos exemplaires est une composante fondamentale pour démontrer la présence d'une paléo-mangrove. *Enigmonia silossa* nov. sp. est comparée aux deux seules autres espèces fossiles connues, *E. bognorensis* Wrigley, 1936 du Cuisien (Yprésien, Éocène inférieur) d'Angleterre et du Lutétien inférieur (Éocène moyen) du bassin de Paris et *E. perplexa* Le Renard, 1990 du Cuisien (Yprésien, Éocène inférieur) du bassin de Paris, ainsi qu'à l'espèce actuelle, *E. aenigmatica* (Holten, 1802).

Mots clés. Mollusca, Bivalvia, Anomiidae, *Enigmonia*, Éocène, Bartonien, bassin d'Aquitaine, Landes, Espèce nouvelle.

Abstract. The new species *Enigmonia silossa* nov. sp., from the Bartonian sandy clay (Middle Eocene) of Horsarrieu [Pédelail] (Landes), is described and figured. This discovery is important for several reasons. First, this is both the first fossil occurrence of the motile Anomiidae *Enigmonia* Iredale, 1918 in the Aquitaine Basin. This is also the first record of the genus in Bartonian (Middle Eocene) sediments and singularly, this is the first specimen with connected valves collected in the fossil record showing a hitherto unknown right valve. The presence and perfect conservation of our specimens is a fundamental component in demonstrating the presence of a paleo-mangrove. The two only other fossil species, *E. bognorensis* Wrigley, 1936 from the Cuisian (Ypresian, Early Eocene) of England and Lutetian (Middle Eocene) of the Paris Basin, and *E. perplexa* Le Renard, 1990 from Cuisian (Ypresian, Early Eocene) of the Paris basin, as well as the recent species, *E. aenigmatica* (Holten, 1802) are compared.

Key words. Mollusca, Bivalvia, Anomiidae, *Enigmonia*, Eocene, Bartonian, Aquitaine Basin, Landes, new species.

Introduction

L'espèce actuelle *Enigmonia aenigmatica* (Holten, 1802) est connue de longue date et avait été figurée sous le nom de *Tellina aenigmatica* dès 1795 (pl. 199, fig. 1949-1950) par CHEMNITZ [Nom établi pour la première fois par Chemnitz dans un ouvrage placé par l'ICZN dans l'Index Officiel des ouvrages rejetés] (**Fig. 1**). *Enigmonia aenigmatica*, appartenant à la famille des Anomiidae, est probablement la coquille la plus caractéristique des mangroves d'Indo-Pacifique ; elle a rarement, voire jamais, été trouvée en dehors de cet écosystème (Yonge, 1957 ; Keen, 1969 : *N*383 ; Berry, 1975 ; Morton, 1976 ; 1983). Elle est largement présente dans les eaux d'Asie du Sud-Est, toujours en association avec des milieux de vie de type mangrove (Yonge, 1977 ; Plaziat, 1995 ; Plaziat *et al.*, 2001 ; Lozouet & Plaziat, 2008). *E. aenigmatica*, une Anomiidae motile [qui a la capacité de se mouvoir activement et spontanément ou par réaction à des stimuli] au test fin et délicat qui vit sur la valve droite de sa coquille, est orientée et positionnée sur les troncs d'arbres d'*Avicennia* et sur les racines aériennes de *Rhizophora*, par rapport à l'axe long de l'arbre et à la direction du courant (**Fig. 2**). La valve supérieure gauche est plus épaisse que la valve inférieure droite et a typiquement la forme d'un cône bas, comme une patelle aplatie. La valve droite est aussi mince qu'une feuille de papier de cigarette et est recouverte par la valve gauche (**Fig. 3**).

Comme chez les autres Anomiidae, *Enigmonia* est fermement fixée par un byssus calcifié, plat et robuste, passant par une grande échancrure circulaire dans la valve droite de la coquille, valve légèrement incurvée, de manière à adhérer étroitement à la surface sur laquelle elle repose. Il en résulte une asymétrie qui revêt une importance particulière pour la compréhension de la morphologie fonctionnelle des organes d'alimentation et de digestion en particulier de ce mollusque (Morton, 1976). Les autres caractères de la coquille sont uniques. L'umbo est situé bien en dessous du bord dorsal, la valve gauche ressemblant à un gastéropode patelliforme (Beu, 1967).

L'espèce actuelle existe sous plusieurs formes de croissance ou morphes (Gray, 1850) résultant des différences anatomiques liées au site de peuplement et de fait, déterminées par la nature de la surface sur laquelle elle s'installe. Morton (1976) a cependant montré qu'il n'existe qu'une seule espèce polymorphe. L'une de ces formes, décrite comme *Anomia naviformis* Jonas, 1847, est brun-pourpre et prend sa forme allongée après s'être fixée sur les tiges étroites, les branches et les racines des *Rhizophora* (voir Yonge, 1977). Une autre, plus petite, de couleur crème, souvent avec un trait de couleur pourpre au niveau de l'umbo, se trouve généralement attachée à la face inférieure des feuilles des pousses d'*Avicennia* et de *Scyphiphora hydrophyllacea*. Une autre forme, décrite comme *Anomia aenigmatica* Holten, 1802 (Berry, 1972 ; 1975), se trouve plus loin dans la mangrove et la coquille est d'un violet profond. Une autre encore, décrite comme *Anomia rosea* Gray, 1825, est grande, arrondie, de couleur pourpre, et se trouve sur la frange maritime de la mangrove.

Enigmonia aenigmatica est donc capable d'une adaptation morphologique subtile à certains des différents microhabitats du système littoral de la mangrove (Morton, 1976). La couleur, la forme et l'épaisseur de la coquille dépendent donc de l'habitat choisi par les individus lors de leur installation. En 1957 encore, Yonge ne savait pas si les individus trouvés sur les tiges et les feuilles étaient des espèces distinctes ou des formes de croissance différentes (Morton, 1976).

La répartition des différents morphes de couleur a donc été observée depuis longtemps : la forme « dorée » (*E. aenigmatica*) [MNHN.F.A97910 et A97911 (coll. Pacaud)], qui a une coquille plus lisse, se trouve sur les feuilles des palétuviers (**Fig. 8-9**), tandis que la forme « brune-violette » [MNHN.F.A97908 et A97909 (coll. Pacaud)], qui a également une surface plus rugueuse (**Fig. 3**), se conformant à la texture de l'écorce ou d'autres substrats sur lesquels elle se développe, se trouve sur les troncs et les branches des palétuviers (Plaziat, 1984), voire sur d'autres substrats durs intertidaux tel que de gros cailloux (en Chine par exemple – comm. pers. J.-C. Plaziat) ; elle a traditionnellement été nommée *Enigmonia rosea* (Gray, 1825). Il semble qu'aucune tentative n'a été faite jusqu'à présent pour expliquer les raisons de l'existence de deux morphes de couleur sur des substrats différents (Sigurdsson & Sundari, 1990 ; Moss, 1993). On notera cependant que de jeunes *Enigmonia aenigmatica* violacés transférés sur des feuilles développent une coquille jaune doré, tandis que les juvéniles jaunes produisent une coquille violette lorsqu'ils poussent sur d'autres substrats que les feuilles de mangrove. Cela prouve que les deux formes de couleur ne sont pas des espèces distinctes. Une analyse des pigments trouvés dans la coquille des deux formes de couleur indique que les pigments violets sont des uroporphyrines. Aucun pigment ne semble être présent dans les coquilles jaune doré (Sigurdsson & Sundari, 1990 ; Ganguly *et al.*, 2020).

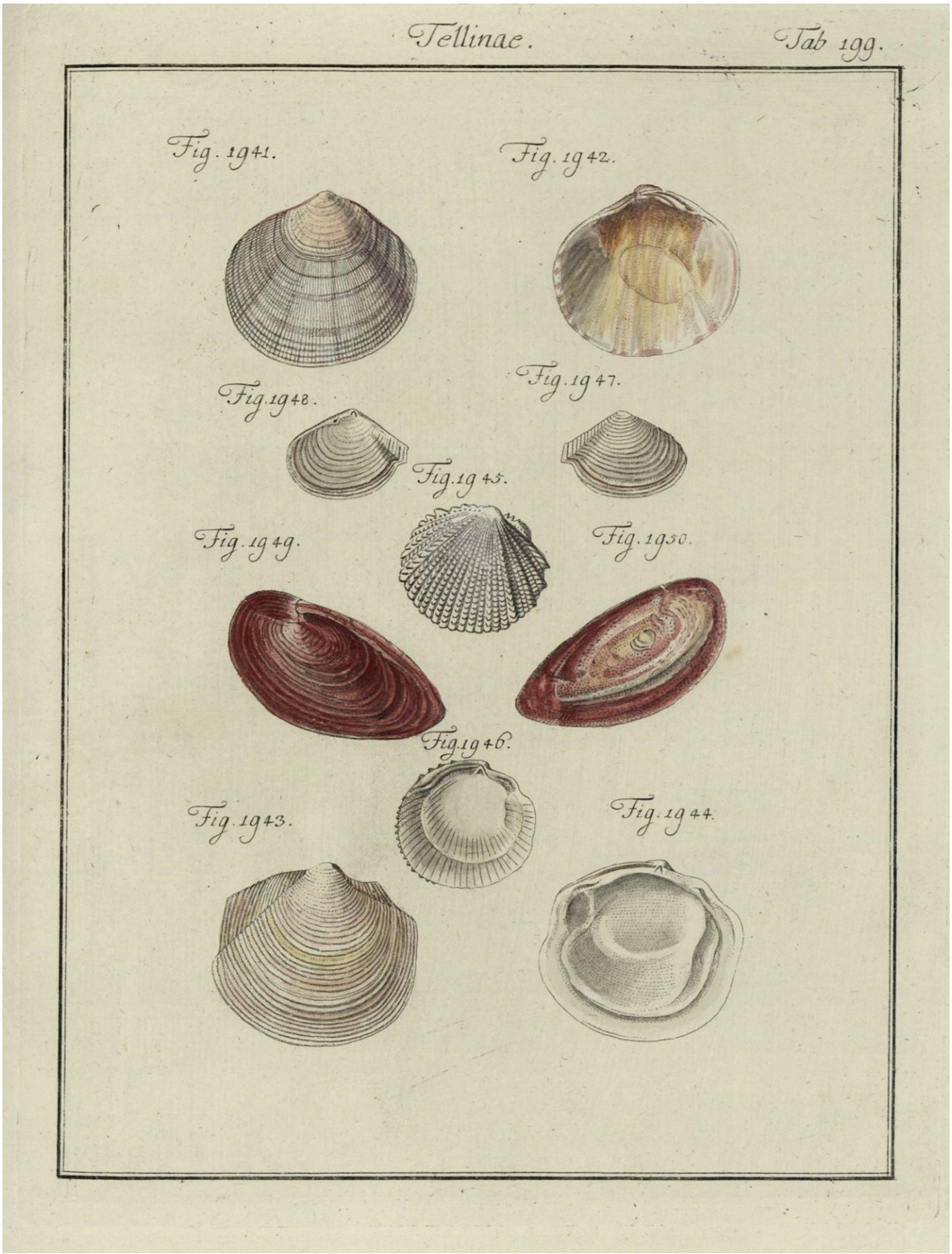
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Figure 1. Planche 199 (fig. 1949-1950) du travail de CHEMNITZ (1795) illustrant l'espèce actuelle *Enigmonia aenigmatica* (Holten, 1802).

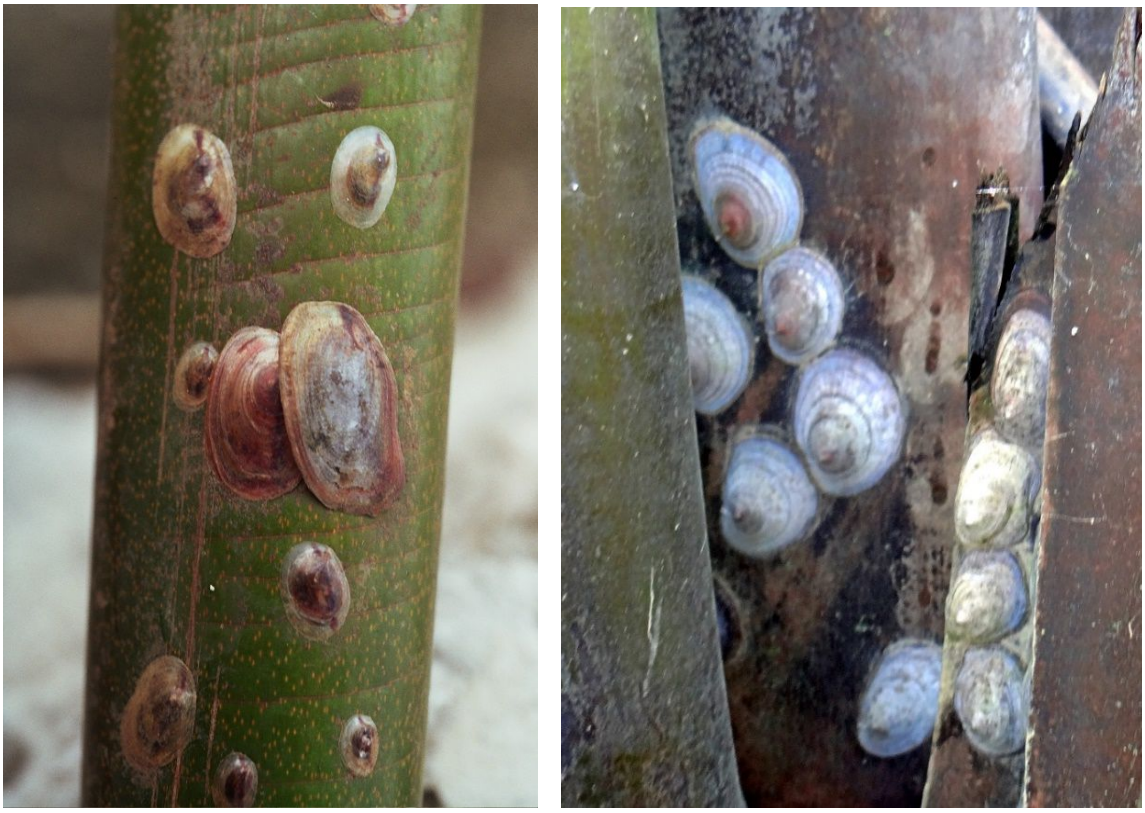

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Figure 2. ***Enigmonia aenigmatica*** (Holten, 1802). **1.** Rivière Abatan, Ile de Bohol (Philippines) (Photo Jean-Claude Plaziat). – **2.** Hội An, Quang Nam (Viêt Nam) (Photo Nico Vromant).

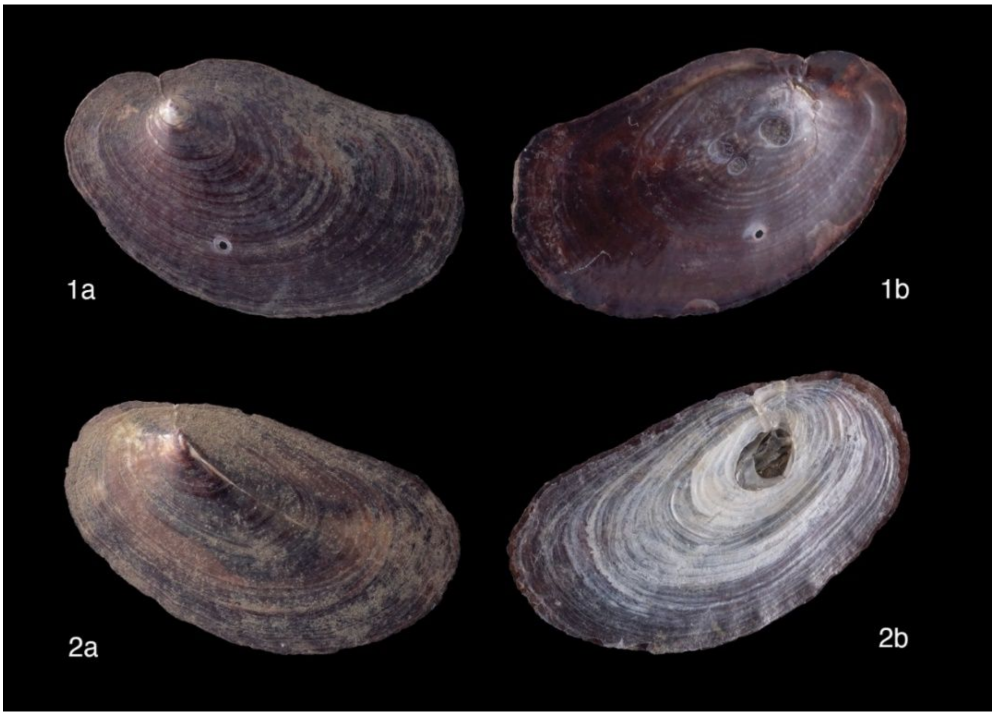

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Figure 3. ***Enigmonia aenigmatica*** (Holten, 1802), provenant de Danao (Ile de Cebu, Philippines). **1a-b.** Valve gauche, MNHN.F.A97908 (coll. Pacaud), longueur : 36,9 mm. **– 2a-b.** Spécimen en connexion, MNHN.F.A97909 (coll. Pacaud), longueur : 36,6 mm.

Les individus vivant sur les feuilles sont motiles, se déplaçant en rampant au moyen d'un pied extensible, long, étroit et aplati, qui fait saillie à travers l'échancrure byssale de la valve droite. Ceux qui vivent sur les tiges et les racines semblent être attachés de façon plus permanente, étant orientés selon leurs axes longs afin de s'adapter à leur substrat. Certaines de ces formes ont été décrites comme des espèces distinctes, respectivement par GRAY [*Anomia rosea* – Taxon invalide : homonyme primaire plus récent de *Anomia rosea* Mawe, 1823], par ANTON [*Anomia aenigmatica*], par KOCH [*Aenigma convexum, Aenigma corrugatum, Aenigma reticulatum*], par JONAS [*Anomia naviformis*] et par TURTON [*Anomia alfredensis, Anomia curiosa, Anomia farquhari, Anomia oblonga*], toutes considérées actuellement comme des synonymes subjectifs de *E. aenigmatica* (Holten, 1802) ; le nom *Anomia aenigmatica* introduit par Anton est de surcroit un homonyme primaire plus récent de *Anomia aenigmatica* Holten, 1802 (GRAY, 1825 : 139 ; ANTON, 1837 : 285 ; KOCH, 1846 : 62-64 ; JONAS, 1847 : 121 ; TURTON, 1932 : 225).

Tous les autres Anomiidae sont généralement arrondis mais, comme BOURNE (1907 : 255) l'a fait remarquer, chez *Enigmonia*, « *l'axe dorso-ventral* » (le pied étant considéré comme antérieur) « *a été tourné d'un angle de 40° dans une direction postéro-antérieure* ». Ceci est indiqué par la direction de l'umbo et la ligne de fusion supradorsale de la valve [**fs**]. On observe alors une coquille étendue postérieurement deux fois plus longue que large (**Fig. 4**).

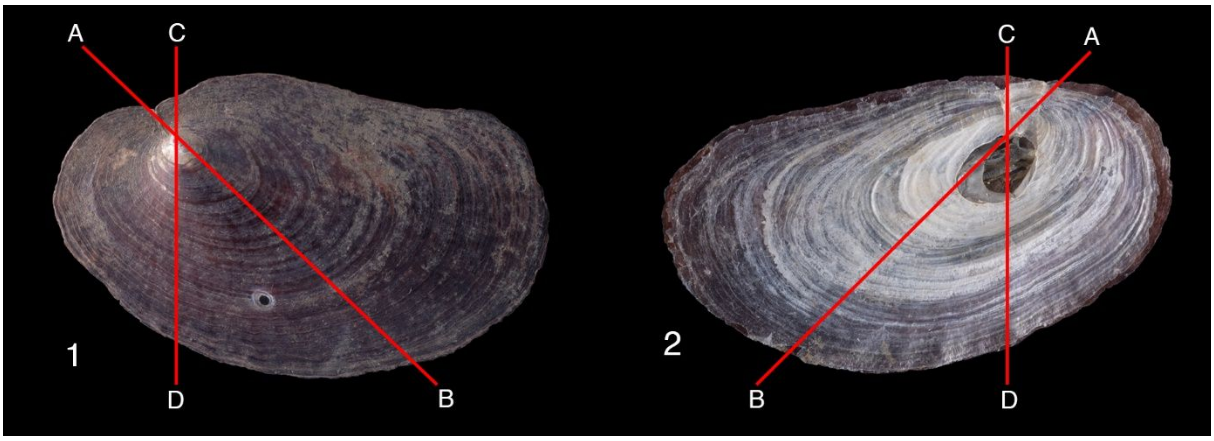

Figure 4. ***Enigmonia aenigmatica*** (Holten, 1802) provenant de Danao (Ile de Cebu, Philippines). **1.** Valve gauche, MNHN.F.A97908 (coll. Pacaud), longueur : 36,9 mm. **– 2.** Valve droite d'un spécimen en connexion, MNHN.F.A97909 (coll. Pacaud), longueur : 36,6 mm. **A-B** : Axe dorso-ventral correct de la coquille. **C-D** : Axe dorso-ventral apparent de la coquille.

La famille des Anomiidae comprend en France à l'Éocène trois genres : *Anomia* Linnaeus, 1758 (Espèce type : *Anomia ephippium* Linnaeus, 1758 par désignation subséquente – SCHMIDT, 1818), *Heteranomia* Winckworth, 1922 (Espèce type *Anomia squamula* Linnaeus, 1758 par désignation originale) et *Enigmonia* Iredale, 1918 (Espèce type : *Anomia rosea* Gray, 1825 par désignation originale [= *Anomia aenigmatica* Holten, 1802]). Les espèces fossiles d'*Anomia* sont nombreuses et relativement courantes dans tout l'Éocène ; plusieurs exemplaires de l'espèce *Anomia psamatheis* Bayan, 1870 [MNHN.F.J07480, (coll. Cossmann)] ont été récoltés à Horsarrieu [Pédelail] (COSSMANN, 1922 : 215, fig. 13, pl. 14, fig. 23 ; pl. 15, fig. 23-25 ; FABRE, 1939 : 241) (**Fig. 5**). Fabre signalait dans ce gisement trois espèces différentes d'*Anomia*, outre *A. psamatheis* Bayan, 1870, il citait *A. tenuistriata* Deshayes, 1832 [= *A. anomialis* Lamarck, 1819] et *A. planulata* Deshayes, 1858. Cependant, on ne peut tirer aucun caractère diagnostique essentiel de la forme et de la convexité des valves, attendu que la coquille peut être plate, convexe ou même enroulée cylindriquement selon son habitat.

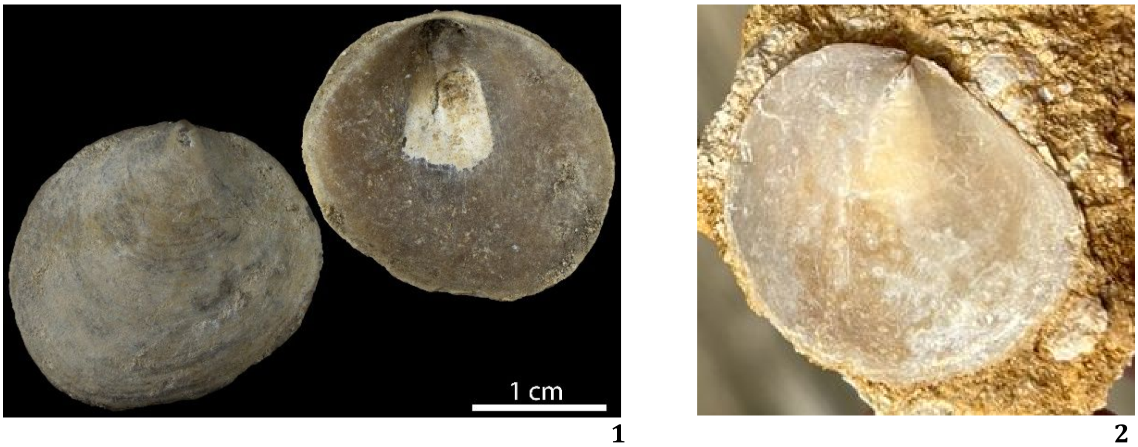

Figure 5. ***Anomia psamatheis*** Bayan, 1870. Bartonien (Éocène moyen) de Horsarrieu [Pédelail] (Landes). **1.** MNHN.F.J07480 (coll. Cossmann), longueur : 23,5 mm. – **2.** MNHN.F.A98958 (coll. Coppini), longueur : 25,5 mm.

Le genre *Heteranomia* est plus rare ; l'examen de spécimens bien conservés de la minuscule *Anomia echinulata* Deshayes, 1858 de l'Auversien (Bartonien, Éocène moyen) de Saint-Witz [Le Guépelle] (Val d'Oise) [MNHN.F.A81022 (coll. Pacaud), MNHN.F.A91674 (coll. Houdas)] révèlent que la valve gauche présente deux traces d'insertion musculaire contiguës (muscle du rétracteur byssal et du muscle adducteur), comme c'est le cas chez l'espèce type d'*Heteranomia*, plutôt que les trois empreintes qui caractérisent *Anomia*. De fait, nous avons assigné *Anomia echinulata* Deshayes, 1858 au genre *Heteranomia* (voir PACAUD *in* COAN *et al.*, 2024 : 714).

Dans le registre fossile, le genre *Enigmonia* est par contre particulièrement rare. WRIGLEY (1936 : 24, pl. 5, fig. 1-3) est le premier auteur à signaler une espèce fossile, *E. bognorensis* Wrigley, 1936, d'après une valve gauche provenant des marnes de l'Yprésien (London Clay, Éocène inférieur) de Rose Green, près de Bognor Regis (Sussex, Angleterre) (DAVIES & ELLIOTT, 1957 : 265 ; CHANDLER, 1961 : 30). D'autres exemplaires [BMNH LL41435 et LL41436 (coll. Symonds)], toujours des valves gauches, ont par la suite été récoltés dans les marnes yprésiennes (Wittering Formation, Éocène inférieur) de Bracklesham Bay, dans les sables du Lutétien inférieur de Chaumont-en-Vexin [Carrière Darcy] (Oise, France) [MNHN.F.A96470, A96471 et A96472 (coll. Pillon)] (MAILLE, 2011) et dans les sables bartoniens de Saffré [Bois-Gouët] (Loire-Atlantique) (**Pl. 1**). Notons également le commentaire de WRIGLEY (1936 : 24-25) selon lequel un exemplaire de l'Yprésien (London Clay, Éocène inférieur) de Highgate (Grand Londres, Angleterre) est figuré sur une planche d'un travail non publié du géologue anglais Nathaniel Thomas Wetherell. Cette petite valve gauche de 22,0 mm, qui serait conservée dans les collections du BMNH et dont l'étiquette de la main de Wetherell indiquait « *Parmaphorus* » [comme un gastropoda donc], est pour Wrigley clairement conspécifique d'*E. bognorensis*.

Plus récemment, LE RENARD (1990 : 92-95, fig. 11-13), LE RENARD & PACAUD (1995 : 85) et PACAUD & LE RENARD (1995 : 177) signalent une seconde espèce fossile du Cuisien (Yprésien, Éocène inférieur) d'après une valve gauche provenant de Parfondru (Aisne), *E. perplexa* Le Renard, 1990 [Holotype MNHN.F.A88680 (coll. Le Renard)] (**Fig. 6**). Depuis, de rares nouveaux exemplaires, toujours des valves gauches, ont été récoltés dans les sables cuisiens (Yprésien, Éocène inférieur) de Liancourt-Saint-Pierre [La Ballastière] (Oise) [MNHN.F.A91673 (coll. Houdas)], de Celles-sur-Aisne (Aisne) [MNHN.F.A91967 (coll. Pacaud)], de Laversine (Aisne) [MNHN.F.A88509 (coll. Pacaud)] (**Pl. 1**) et de Saint-Gobain [MNHN.F.A96473 (coll. Faullummel)]. Toutes ces coquilles sont de dimensions modestes alors que les spécimens de Horsarrieu [Pédelail], provenant des argiles sableuses bartoniennes, que nous décrivons ici sont relativement grandes et peuvent atteindre une longueur de 73,2 mm. Cependant, concernant le bassin d'Aquitaine, nous n'avons trouvé aucune observation concernant l'espèce discutée ici dans les courtes listes plus ou moins inspirées des coquilles du bassin de Paris dans les articles de BENOIST (1887), de LAMBERT (1914), d'ABRARD (1931), de LARROUDE (1967) ou de FABRE (1939).

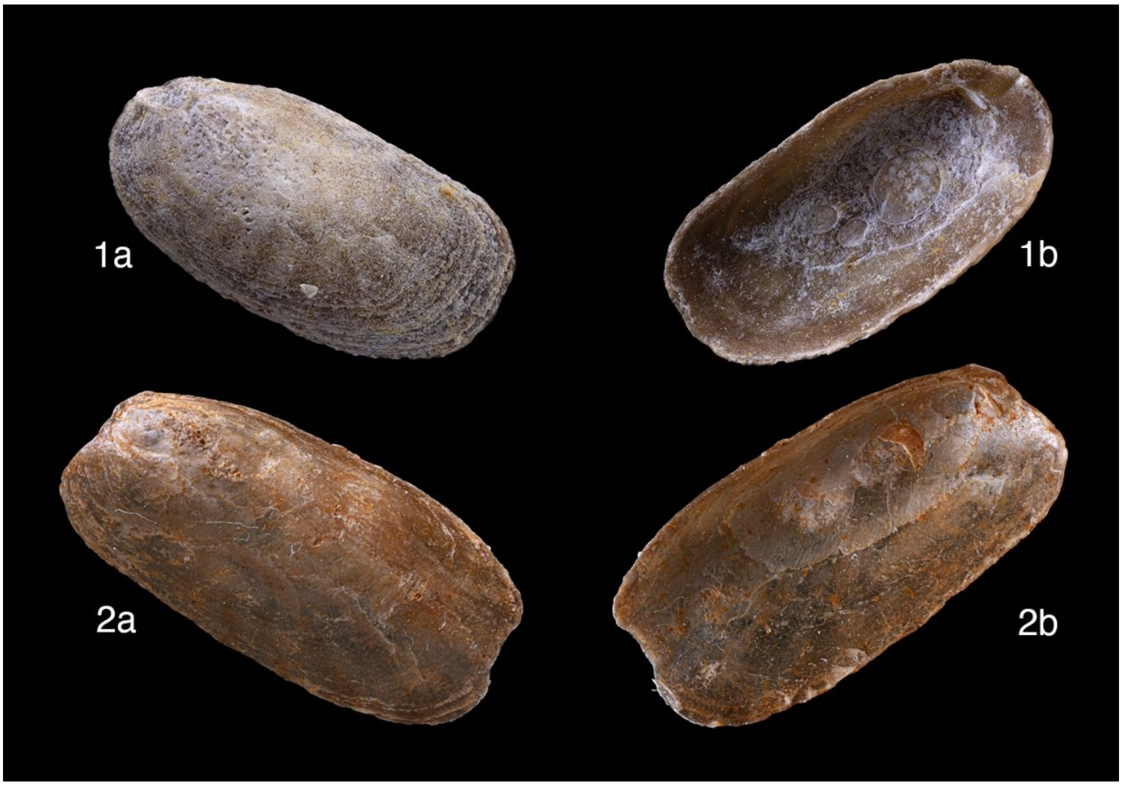

Figure 6. *Enigmonia perplexa* Le Renard, 1990. **1a-b.** Yprésien (Cuisien, Éocène inférieur) de Parfondru (Aisne) Holotype MNHN.F.A88680 (coll. Le Renard), longueur : 7,8 mm. – **2a-b.** Yprésien (Cuisien, Éocène inférieur) de Laversine (Aisne), MNHN.F.A88509 (coll. Pacaud), longueur : 18,6 mm.

Dans son Synopsis des mollusques du bassin d'Aquitaine, étude qui complète alors la première étape en cours de publication sur le Néogène du bassin d'Aquitaine, COSSMANN (1921 ; 1922) entreprend l'étude des bivalves de l'Éocène et de l'Oligocène des gisements de la même région. Dans cet important mémoire, dans lequel il passe en revue tous les bivalves, depuis le Cuisien (Éocène inférieur) jusqu'au Rupélien (Oligocène inférieur), Cossmann ne fait aucune mention de notre coquille ; il semble donc que l'exploration du gisement de Pédelail par Marcel Neuville, qui a fourni une faune de bivalve importante à partir de laquelle l'auteur a travaillé, n'ait pas permis de récolter ces valves d'*Enigmonia*. Nous n'avons par ailleurs observé aucun spécimen, même fragmentaire, dans la collection Neuville conservée à l'Université de Bordeaux, à Talence.

Matériel et méthode

Les exemplaires discutés ici se distinguent très nettement des deux seuls autres taxons fossiles connus, *Enigmonia bognorensis* Wrigley, 1936 du Cuisien (Yprésien, Éocène inférieur) et du Lutétien inférieur (Éocène moyen) et *Enigmonia perplexa* Le Renard, 1990 du Cuisien (Yprésien, Éocène inférieur) par des caractères constants. Malheureusement, une partie de ce matériel [MNHN.F.A88509 (coll. Pacaud), MNHN.F.A96473 (coll. Faullummel), MNHN.F.A91673 (coll. Houdas), MNHN.F.A96470, A96471 et A96472 (coll. Pillon)] n'a pu être actuellement localisée (**Pl. 1**). Par ailleurs, la découverte à Pédelail d'un exemplaire parfaitement conservé les valves en connexion, nous permet pour la première fois de décrire dans le registre fossile une valve droite d'*Enigmonia*. Nous avons déjà décrit de ce gisement (PACAUD *et al.*, 2024a-b) deux autres espèces nouvelles à l'issue de la campagne de fouille de 2021/2022, *Pachycrommium gourguesi* Pacaud, Buisson, Coppini & Meunier, 2024, seconde espèce de *Pachycrommium* décrite dans le Bartonien du bassin d'Aquitaine ; taxon que nous pensions endémique du gisement de Pédelail, mais qui existe également dans les sédiments bartoniens d'Espagne (GOMEZ GARCIA, 2024 : 281, figuré sous le nom erroné de *Ampullinopsis crassatina*) et *Pseudomiltha horcsarriu* Pacaud, Coppini, Buisson & Meunier, 2024, seconde plus grande espèce de *Pseudomiltha* décrite à l'Éocène en France, montrant tout l'intérêt du site de Pédelail. Ce Lucinidae a été récolté (coll. Remy) récemment dans les sables bartoniens de Campbon (Loire-Atlantique). Les niveaux exploités lors des fouilles à Pédelail ont actuellement disparu.

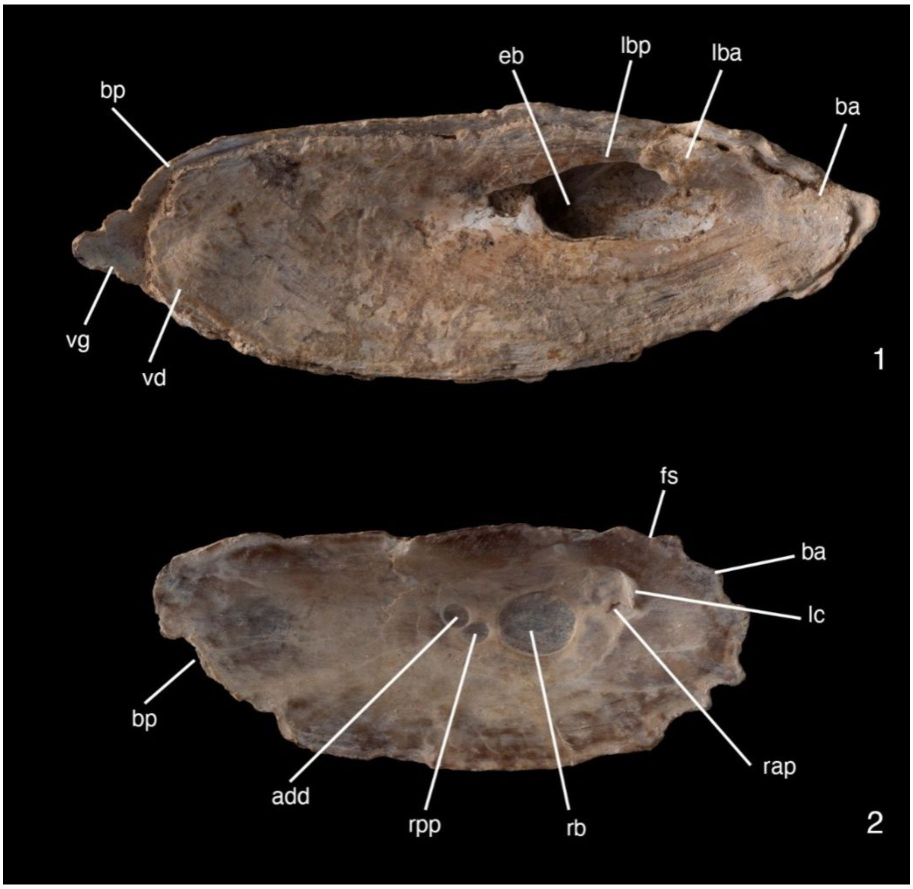

Figure 7. ***Enigmonia silossa*** nov. sp. Bartonien (Éocène moyen) de Horsarrieu [Pédelail] (Landes). Termes utilisés désignant les principaux caractères de la coquille. **1.** Paratype (spécimen en connexion), MNHN.F.A97905 (coll. Coppini). – **2.** Paratype (valve gauche), MNHN.F.A97907 (coll. Coppini). **ba** : bord antérieur, **bp** : bord postérieur, **fs** : fusion supradorsale, **eb** : échancrure byssale, **lba** : lobe du bord antérieur de la valve droite, **lbp** : lobe du bord postérieur de la valve droite, **lc** : lame chondrophore, **add** : trace d'insertion du muscle adducteur, **rpp** : trace d'insertion du muscle rétracteur postérieur du pied, **rb** : trace d'insertion du muscle rétracteur byssal, **rap** : trace d'insertion du muscle rétracteur antérieur du pied, **vd** : valve droite, **vg** : valve gauche.

Abréviations des références aux collections.

BMNH	Department of Palaeontology, The Natural History Museum, Londres, Angleterre.
MNHN.F	Muséum National d'Histoire Naturelle, Collection de Paléontologie, Paris, France.
MNHN.IM	Muséum National d'Histoire Naturelle, Collection de Malacologie, Paris, France.

Autres abréviations.

ba	bord antérieur.
bp	bord postérieur.
u	umbo ou crochet.
fs	fusion supradorsale.
eb	échancrure byssale.
lba	lobe du bord antérieur de la valve droite.
lbp	lobe du bord postérieur de la valve droite.
lc	lame chondrophore (ou crura).
add	trace d'insertion du muscle adducteur.
rpp	trace d'insertion du muscle rétracteur postérieur du pied.
rb	trace d'insertion du muscle rétracteur byssal.
rap	trace d'insertion du muscle rétracteur antérieur du pied.
vd	valve droite.
vg	valve gauche.

Systématique

Classe **Bivalvia** Linnaeus, 1758
Sous-classe **Autobranchia** Grobben, 1894
Infra-classe **Pteriomorpha** Beurlen, 1944
Ordre **Pectinida** Gray, 1854
Super-famille Anomioidea Rafinesque, 1815
Famille Anomiidae Rafinesque, 1815
Genre ***Enigmonia*** Iredale, 1918

Espèce type : *Anomia rosea* Gray, 1825 (*non* Mawe, 1823) par désignation originale
[= *Anomia aenigmatica* Holten, 1802]
Origine : Australie, Récent

Synonymie
Aenigma Koch, 1846. Taxon invalide : homonyme primaire plus récent de *Aenigma* Neuman, 1836 [Coleoptera].

Enigmonia silossa **nov. sp.**

(Fig. 7 ; pl. 2-3)

https://zoobank.org/NomenclaturalActs/81164962-4DE0-4D0C-9FF8-6BA345722309

Matériel-type. Holotype (valve gauche) MNHN.F.A97902 (coll. Coppini), paratypes : 6 ex. (valves gauches), MNHN.F.A97903, A97904, A97906 et A97907 (coll. Coppini), 1 ex. MNHN.F.A98957 (coll. Audouit), 1 ex. (spécimen aux valves en connexion), MNHN.F.A97905 (coll. Coppini).
Localité type. Horsarrieu [Pédelail] (Landes).
Étage type. Bartonien (Éocène moyen), argiles sableuses de la base du Calcaire de Brassempouy (Capdeville, 1997).
Étymologie. La localité type est située en Chalosse, terroir de Gascogne situé dans le sud du département français des Landes. Le nom de ce terroir apparaît sous la forme *Silossa* en 1270 (Pon & Cabanot, 2010 : 492). Nom donné en apposition.
Autre matériel examiné. 6 ex. (valves gauches, coll. Coppini), 9 ex. incomplets (valves gauches, coll. Buisson), 4 ex. (valves gauches, coll. Audouit).
Dimensions.
Paratype MNHN.F.A97903 (valve gauche). Longueur : 73,2 mm. – Largeur : 20,5 mm.
Paratype MNHN.F.A97904 (valve gauche). Longueur : 71,0 mm. – Largeur : 19,6 mm.
Holotype MNHN.F.A97902 (valve gauche). Longueur : 70,0 mm. – Largeur : 22,5 mm.
Paratype MNHN.F.A97905, Spécimen en connexion (valve gauche). Longueur : 66,2 mm. – Largeur : 22,2 mm. (valve droite). Longueur : 57,2 mm. – Largeur : 20,2 mm.
Paratype MNHN.F.A98957 (valve gauche). Longueur : 53,3 mm. – Largeur : 16,2 mm.
Paratype MNHN.F.A97906 (valve gauche). Longueur : 50,1 mm. – Largeur : 16,5 mm.
Paratype MNHN.F.A97907 (valve gauche). Longueur : 48,8 mm. – Largeur : 20,1 mm.
Description.
(Valve gauche). La coquille est de grande taille, modérement épaisse, transverse, étroitement allongée, inéquilatérale, convexe, presque aussi large d'un côté que de l'autre. Le bord antérieur est court, obtus, festonné par quelques côtes, larges, rayonnantes de l'umbo, séparées par des intervalles larges et légèrement concaves, au fond desquels on distingue des stries d'accroissement lamelleuses et transverses qui se relèvent sur les côtes. Le bord postérieur est long, rostré à son extrémité en raison d'une carène dorsale formant un bourrelet large, saillant et rectiligne qui dépasse le bord palléal sans s'adoucir. La face externe est d'aspect mat, de couleur ambrée, ridée par des stries d'accroissement régulières, lamelleuses et extrêmement fines. De très nombreuses stries rayonnantes, très fines et très serrées, couvrent par ailleurs la surface dorsale. Le stade juvénile de la coquille est délimité par un arrêt de croissance nettement marqué et de forme elliptique. On observe des traces de la coloration d'origine constituées de très nombreuses rayures sombres, au contour tremblé, partant de la carène dorsale et rayonnant vers la périphérie de la coquille. La carène dorsale est bien délimitée par une bande linéaire d'une teinte plus sombre que le reste de la coquille [comme on peut l'observer sur quelques coquilles de l'espèce actuelle *Enigmonia aenigmatica*

(Holten, 1802) (**Fig. 9**)]. L'umbo [**u**], bien visible, peu saillant, largement émoussé, pointant en diagonale vers le bord dorsal antérieur, est situé au quart de la longueur totale. On distingue sur la partie antérieure de la coquille, dans le prolongement de l'umbo, une petite côte à peine saillante, de teinte brune, rayonnant vers le bord dorsal de la valve et correspondant à la fusion supradorsale [**fs**] des bords dorsaux antérieur et postérieur de la coquille. Cette petite côte montre des lignes d'accroissements curvilignes, très épaisses, irrégulièrement réparties (rappelant les lignes d'accroissements du cal d'obturation de la sélénizone des Gastropoda Emarginulinae). L'échancrure de cette côte est à peine visible sur le bord dorsal. La face interne, creuse, en forme de gouttière, de couleur ambrée, montre dans la partie centrale de la coquille, une zone de teinte légèrement plus claire, délimitée par un sillon irrégulier. Au niveau de la dépression umbonale on distingue une lame chondrophore **[lc]** blanchâtre pointant vers le bord ventral et dans le prolongement de cette crura, plus ou moins perpendiculaire à celle-ci, une légère encoche sur le bord dorsal de la valve correspondant à la fusion supradorsale [**fs**]. Les impressions musculaires sont très nettement visibles, profondes, gravées dans le test. On distingue ainsi, dans la région centrale de la coquille, l'empreinte la plus grande, subcirculaire, correspondant à la trace d'insertion du muscle rétracteur byssal [**rb**]. Deux cicatrices, peu visibles, divergentes de chaque côté de l'empreinte, orientées vers l'umbo, délimitent les positions successives du point d'attache du muscle. Juste en-dessous de la lame chondrophore on aperçoit l'impression correspondant au point d'attache du muscle rétracteur antérieur du pied [**rap**], petite, ovalaire et déprimée. Enfin, on distingue la trace d'insertion du muscle adducteur [**add**] située à peu près au milieu de la valve et celle du muscle rétracteur postérieur du pied [**rpp**] ; empreintes ovalaires, égales, plus petites que celle du muscle rétracteur byssal.

(Valve droite). La coquille est de grande taille, modérement épaisse, transverse, étroitement allongée, inéquilatérale, presque aussi large d'un côté que de l'autre, nettement incurvée, de manière à adhérer étroitement à la surface sur laquelle elle repose, épousant étroitement le galbe interne de la valve gauche. Le bord antérieur est court, obtus. Le bord postérieur est long, arrondi à son extrémité. La face externe est blanchâtre, ridée par de nombreuses stries d'accroissement régulières, lamelleuses et extrêmement fines. On distingue une extension supradorsale très importante mais aucune trace d'umbo. En raison de l'allongement postérieur, on observe un net recouvrement du bord dorsal au-dessus de l'échancrure byssale [**eb**] de sorte que l'ouverture de celle-ci est grande, large et allongée, complètement fermée. Les surfaces des deux lobes du bord postérieur et antérieur de la coquille ne fusionnent pas ; le lobe du bord antérieur **[lba]**, large, se superpose sur le lobe du bord postérieur **[lbp]**, plus étroit. La face interne n'a pu être observée ; l'unique exemplaire en connexion, trop fragile, ne nous permet pas de séparer les deux valves sans briser la valve droite, extrêmement fine.

Discussion.

Comme chez d'autres bivalves de la famille des Anomiidae, le byssus d'*Enigmonia* a migré dans l'échancrure profonde de la valve droite, de sorte que le bord de la valve gauche appuie directement sur le substrat, comme chez une patelle. Par conséquent, les spécimens qui se sont installés sur les tiges des palétuviers prennent une forme allongée, semblable à une gouttière. Les individus qui se développent sur les feuilles sont plats et moins allongés et peuvent également se mouvoir en déplaçant leur byssus. Les coquilles des exemplaires récoltés dans les argiles sableuses du Bartonien (Éocène moyen) de Horsarrieu [Pédelail] (Landes) sont allongées et prennent la forme d'une gouttière ; ces spécimens se sont assurément développés sur les tiges, les branches ou sur les racines poreuses des palétuviers.

La valve gauche d'*Enigmonia silossa* nov. sp. diffère de celle d'*E. bognorensis* Wrigley, 1936 (sa valve droite est inconnue) de l'Yprésien (Éocène inférieur) d'Angleterre et du Lutétien et du Bartonien (Éocène moyen) du bassin de Paris et de Loire-Atlantique (**Pl. 1**), par ses dimensions nettement supérieures ; le plus grand spécimen de l'espèce de l'Yprésien d'Angleterre mesure 42,0 mm. L'espèce du bassin d'Aquitaine se distingue également par une coquille plus épaisse, plus creuse, moins déprimée, étroitement allongée, presque aussi large d'un côté que de l'autre, par son bord postérieur plus long, rostrée à son extrémité, par la position de la côte correspondant à la fusion supradorsale [**fs**] des bords dorsaux de la coquille, placée dans le prolongement de l'umbo et rayonnant vers le bord dorsal de la valve et non en avant du bord antérieur comme chez *E. bognorensis*. On notera l'absence sur la partie antérieure d'un canal antérieur pouvant exister sur l'espèce de l'Yprésien d'Angleterre (non présente sur l'holotype, mais visible sur un spécimen juvénile [BMNH LL41436 (coll. Symonds)] provenant des marnes yprésiennes de Bracklesham Bay).

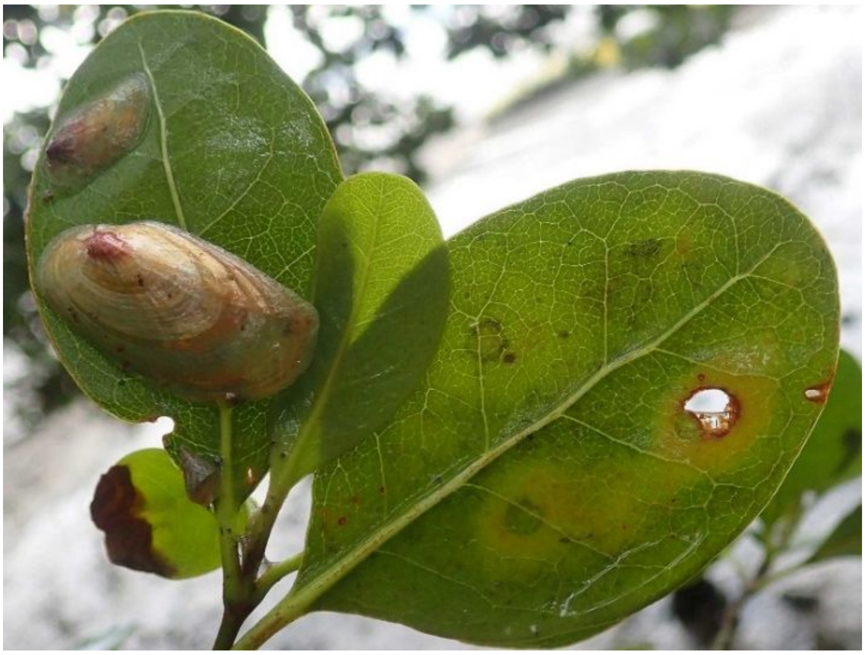

Figure 8. ***Enigmonia aenigmatica*** (Holten, 1802) fixé sur une feuille d'*Avicennia* (Photo Ria Tan).

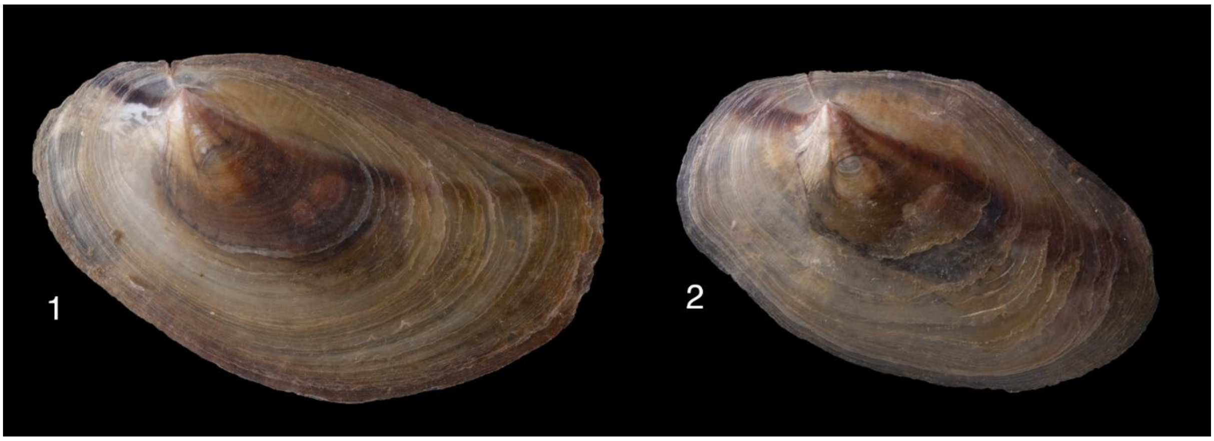

Figure 9. ***Enigmonia aenigmatica*** (Holten, 1802) provenant de Buenavista [Cambuhat], Ile de Bohol (Philippines) montrant sur la face dorsale de la valve gauche une bande linéaire d'une teinte plus sombre que le reste de la coquille. **1.** MNHN.F.A97910 (coll. Pacaud), longueur : 30,0 mm. – **2.** MNHN.F.A97911 (coll. Pacaud), longueur : 25,7 mm.

La valve gauche d'*E. silossa* nov. sp. diffère de celle d'*E. perplexa* Le Renard, 1990 (sa valve droite est également inconnue), de l'Yprésien (Éocène inférieur) du bassin de Paris (**Fig. 6 ; pl. 1**), par ses dimensions très nettement supérieures [l'holotype MNHN.F.A88680 (coll. Le Renard) de l'espèce du bassin de Paris, ne mesure que 7,8 mm de longueur – l'exemplaire de Celles-sur-Aisne (Aisne), MNHN.F.A91967 (coll. Pacaud), mesure 20,0 mm de longueur ; celui de Laversine (Aisne), MNHN.F.A88509 (coll. Pacaud), mesure 18,6 mm de longueur ; celui de Liancourt-Saint-Pierre (Oise), MNHN.F.A91673 (coll. Houdas) mesure 17,0 mm de longueur], par une coquille bien plus épaisse, plus creuse, étroitement allongée, par son bord postérieur plus long, rostrée à son extrémité, par la côte correspondant à la fusion supradorsale des bords dorsaux plus nettement saillante, placée dans le prolongement de l'umbo et rayonnant vers le bord dorsal de la valve (et non par un faible renflement correspondant à un prolongement marginal de la crura comme chez *E. perplexa*), par l'absence sur la partie antérieure d'un « *canal encochant le contour* » (LE RENARD, 1990) formant une gouttière comme sur la coquille du Cuisien du bassin parisien et par la position plus excentrée des traces d'insertions musculaires, le centre de la valve ne tombant pas à l'intérieur de l'empreinte du muscle rétracteur byssal mais plutôt au niveau des traces d'insertions des muscles adducteur et rétracteur postérieur du pied. La coquille montre également des traces plus nettes de la coloration d'origine constituées de plus nombreuses rayures sombres, au contour tremblé et non de faibles faisceaux radiaux.

Bien plus proche de certains morphes de l'espèce actuelle *E. aenigmatica* (Holten, 1802), l'espèce fossile *E. silossa* nov. sp. en diffère par ses dimensions plus importantes. Par une valve gauche plus épaisse, plus creuse, moins déprimée, étroitement allongée, presque aussi large d'un côté que de l'autre, par son bord postérieur plus long, rostrée à son extrémité, par sa carène dorsale formant un bourrelet large, saillant et rectiligne qui dépasse le bord palléal, par ses traces de coloration originale constituées de nombreuses rayures sombres, au contour tremblé. BOURNE (1907 : 257, fig. 1) a observé sur l'espèce actuelle la présence d'une petite trace d'insertion d'un muscle branchial que nous n'avons pas observé sur nos coquilles fossiles (ni par ailleurs, sur les espèces cuisienne et lutétienne). La valve droite de *E. silossa* nov. sp. est relativement proche de celle de l'espèce actuelle ; elle montre surtout une échancrure byssale bien plus grande, bien plus allongée.

Le genre *Enigmonia* n'avait encore jamais été signalé ni dans des sédiments du Bartonien, ni dans le bassin d'Aquitaine, elle n'est cependant pas rare dans le gisement de Pédelail, sans être commune, malgré la fragilité relative de son test, dans des argiles sableuses où la compaction de ces dernières restent importante. La découverte d'*Enigmonia* dans le Bartonien des Landes étend donc considérablement la longévité connue du genre et l'aire de distribution passée de ce genre si restreint jusqu'à présent ; en effet dans le registre fossile, seuls jusqu'ici des spécimens étaient signalés dans le bassin de Paris et en Angleterre à l'Yprésien et au Lutétien inférieur. La découverte d'un spécimen avec sa valve droite est également très importante ; jusqu'ici aucune de ces valves n'avait pu être observée dans le registre fossile, où par ailleurs, les valves gauches sont déjà d'une grande rareté. La finesse extrême de cette valve droite observée par exemple chez l'espèce actuelle *Enigmonia aenigmatica* (Holten, 1802) [MNHN.F.A97909 (coll. Pacaud)] (**Fig. 3***),* aussi fine que du papier à cigarette, explique pourquoi celle-ci n'avait jamais été retrouvée dans des sédiments cénozoïques où elle est vraisemblablement détruite lors de la fossilisation.

YONGE (1977) remarque chez les *Enigmonia* actuelles que contrairement aux individus plats qui sont généralement presque incolores, les organes étant visibles à travers la valve gauche translucide, les spécimens se fixant sur les tiges, sont d'un brun rougeâtre foncé. Notre coquille est de couleur ambrée et présente des traces de la coloration d'origine constituées de très nombreuses rayures sombres, au contour tremblé, partant de la carène anale et rayonnant vers la périphérie de la coquille. L'Anomiidae *Enigmonia* est généralement considéré comme un indicateur fiable d'environnements à mangroves, même si PLAZIAT (1995 : 89) écrit qu'il a collecté des spécimens actuels fixés sous des gravats intertidaux en Chine du Sud.

La découverte dans les argiles sableuses du Bartonien (Éocène moyen) de Horsarrieu [Pédelail] (Landes) et la conservation parfaite de nos exemplaires, ainsi que la présence de plusieurs espèces d'Ellobiinae, de *Cerithideopsis* sp., d'*Isognomon* sp., est une composante fondamentale pour démontrer la présence d'une paléo-mangrove. Nul doute que *Enigmonia silossa* nov. sp. prend sa forme allongée après s'être fixée et se soit développée sur les tiges, les branches ou sur les racines poreuses de palétuviers ; en excluant probablement l'hypothèse peu valorisante de branchages flottés jusqu'au rivage. La découverte de cette espèce nouvelle est importante à plus d'un titre. En premier lieu, c'est la première occurrence fossile de l'Anomiidae *Enigmonia* Iredale, 1918 dans le bassin d'Aquitaine. C'est également le premier signalement de ce genre dans des sédiments du Bartonien (Éocène moyen) et singulièrement, c'est le premier exemplaire aux valves en connexion récolté dans le registre fossile montrant ainsi une valve droite, jusqu'ici inconnue.

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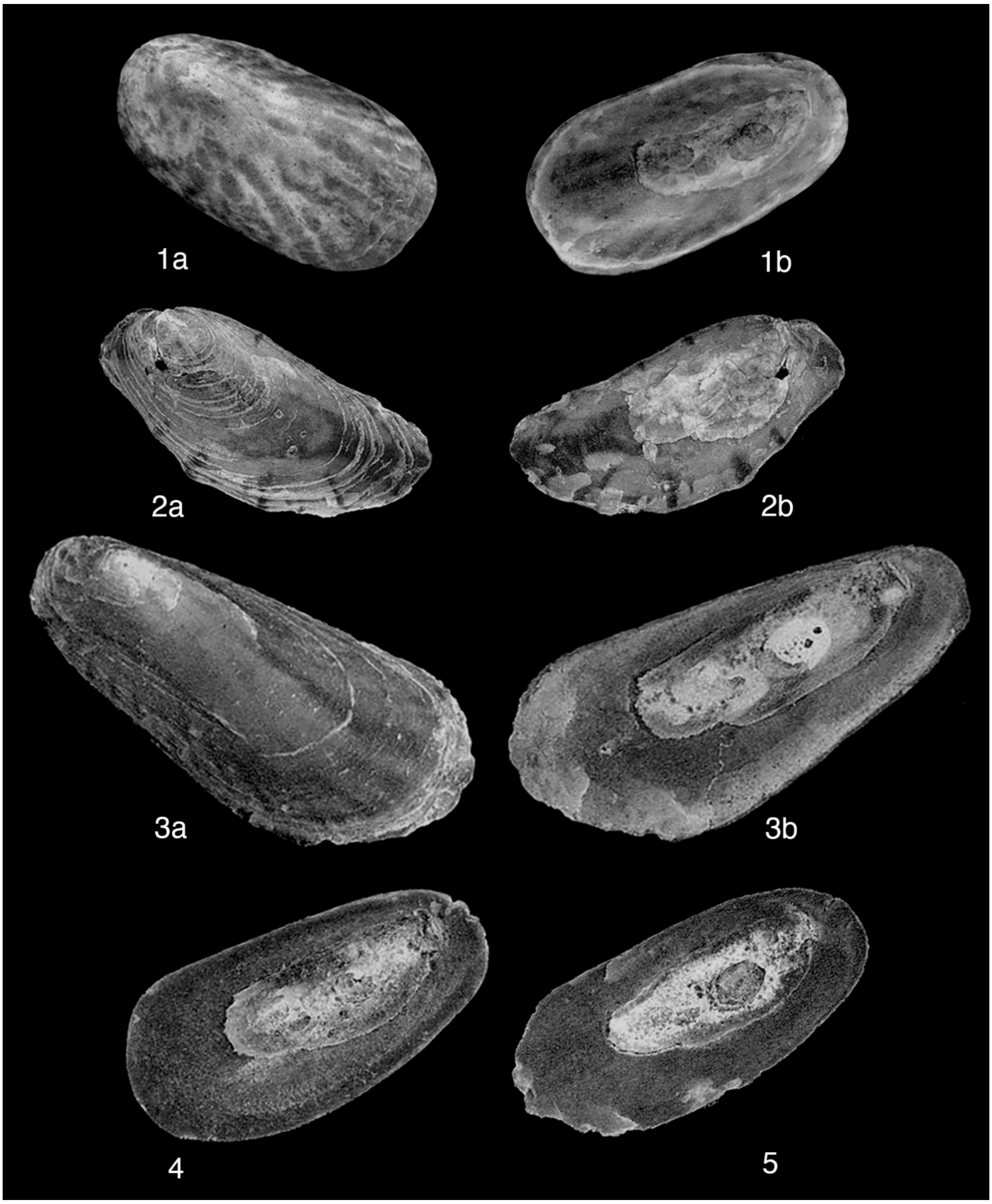

Planche 1. 1a-b. ***Enigmonia perplexa*** Le Renard, 1990. Yprésien (Cuisien, Éocène inférieur) de Celles-sur-Aisne (Aisne), MNHN.F.A91967 (coll. Pacaud), longueur : 20,0 mm. – **2-5.** ***Enigmonia bognorensis*** Wrigley, 1936. **2a-b**. Bartonien (Éocène moyen) de Saffré [Bois-Gouët] (LoireAtlantique), longueur : 23,0 mm. – **3-5.** Lutétien inférieur (Éocène moyen) de Chaumont-en-Vexin [Carrière Darcy] (Oise), **3a-b.** MNHN.F.A96470 (coll. Pillon), longueur : 29,0 mm. – **4.** MNHN.F.A96471 (coll. Pillon), longueur : 22,5 mm. – **5.** MNHN.F.A96472 (coll. Pillon), longueur : 20,0 mm.

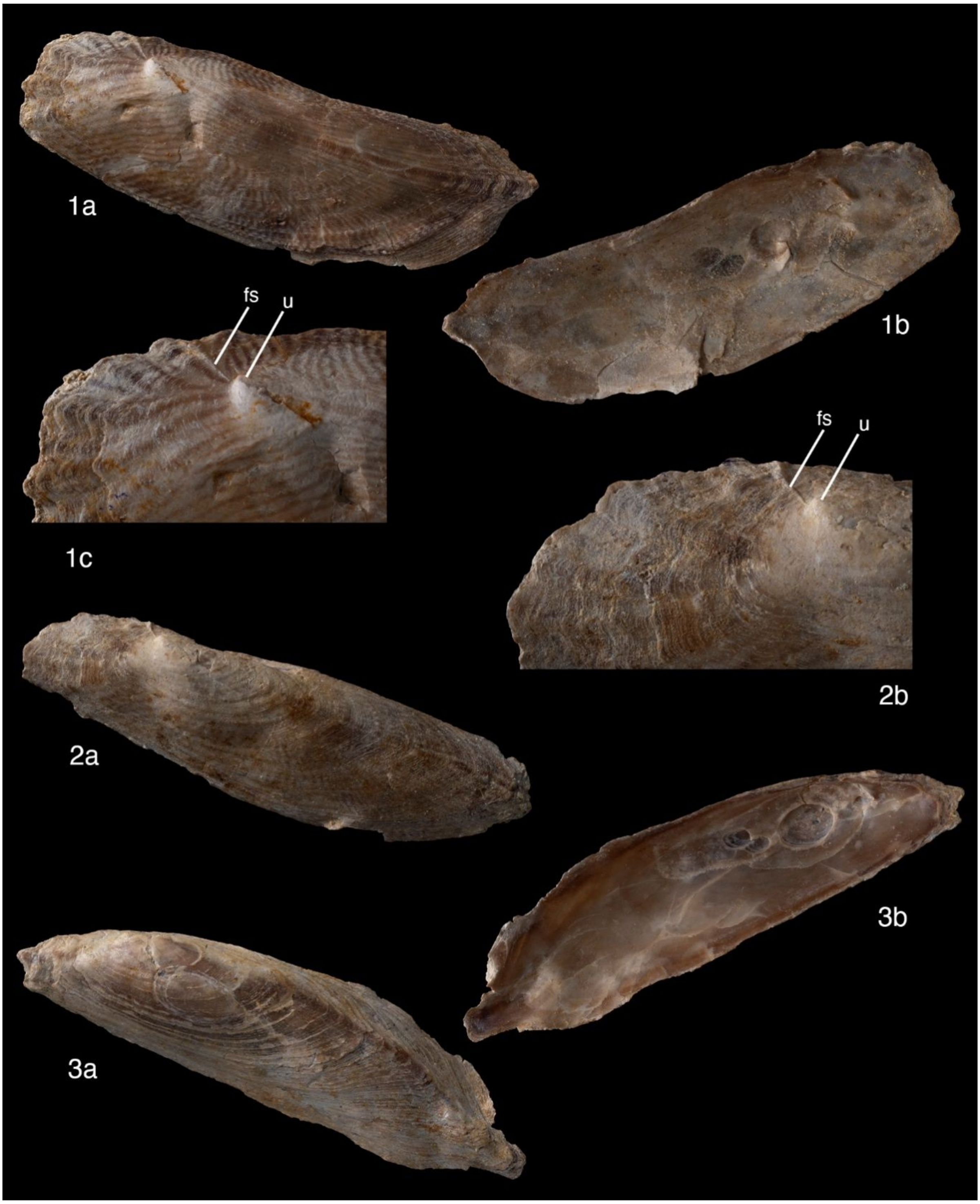

Planche 2. ***Enigmonia silossa*** nov. sp. Bartonien (Éocène moyen) de Horsarrieu [Pédelail] (Landes). **1a-c**. Holotype (valve gauche) MNHN.F.A97902 (coll. Coppini), longueur : 70,0 mm. – **2a-b.** Paratype (valve gauche), MNHN.F.A97904 (coll. Coppini), longueur : 71,0 mm. – **3a-b.** Paratype (valve gauche), MNHN.F.A97903 (coll. Coppini), longueur : 73,2 mm. **u** : umbo, **fs** : fusion supradorsale.

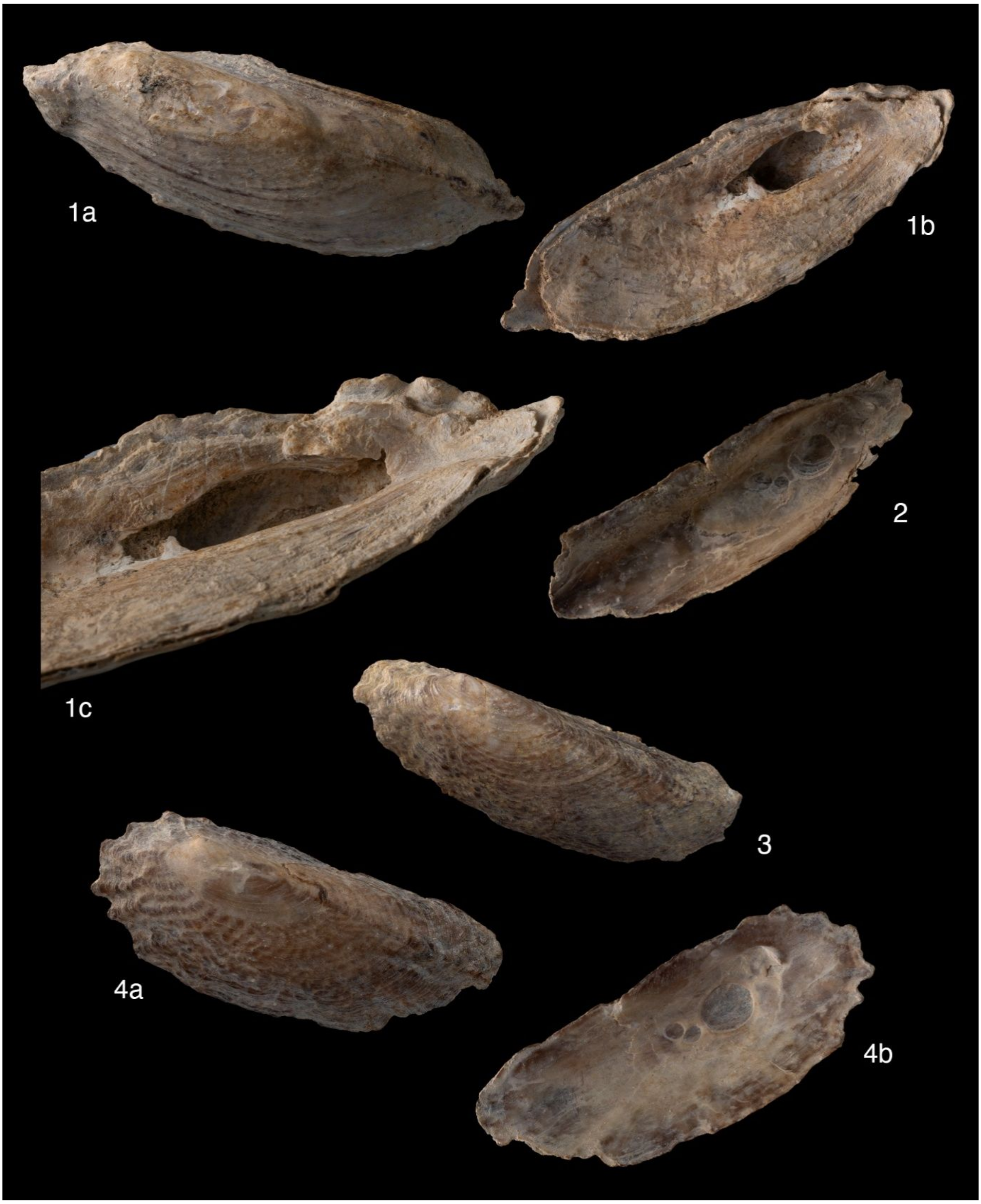

Planche 3. ***Enigmonia silossa*** nov. sp. Bartonien (Éocène moyen) de Horsarrieu [Pédelail] (Landes). **1a-c**. Paratype (spécimen en connexion), MNHN.F.A97905 (coll. Coppini), **1a** (valve gauche), longueur : 66,2 mm, **1b** (valve droite), longueur : 57,2 mm., **1d.** Détail de l'échancrure byssale montrant la superposition du lobe antérieur sur le lobe postérieur – **2.** Paratype (valve gauche), MNHN.F.A98957 (coll. Audouit). – **3.** Paratype (valve gauche), MNHN.F.A97906 (coll. Coppini), longueur : 50,1 mm. – **4a-b.** Paratype (valve gauche), MNHN.F.A97907 (coll. Coppini), longueur : 48,8 mm.

Corrections : Tello Neckheim 2025 The terrestrial snails from île Tintamarre (Saint-Martin, French Antilles). *Folia Conchyliologica,* 75 : 1-11.

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[1] cmneckheim@gmail.com

Since the publicarion of article on Tintamarra remained dormant for some time, some of the nomenclature has changed, and I failed to update it accordingly.

- *Cecilioides aperta*: The taxon *aperta* is the type species of the genus *Geostilba*. The correct name should therefore be *Geostilba aperta*.
- *Pupoides albilabris*: This is generally considered to be a synonym of *Pupoides nitidulus* (L. Pfeiffer, 1839).
- *Chondropoma pupiforme*: The author is *G.B. Sowerby **I***, not *G.B. Sowerby **II**.*
- *Drymaeus virgulatus*: The correct name is *Drymaeus elongatus* (Roding, 1798) (see: Bank, 2022).
- *Lissachatina fulica* (page 9): The author should be (Bowdich, 1822), not (A. Férussac, 1821).